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MAZE STUDIES WITH THE WHITE RAT

II. BLIND ANIMALS

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In the previous paper there was formulated the proposition that the maze habit is dependent to some degree upon the stability of various environmental conditions. The present paper concerns the function vision in sensing these alterations and becoming adapted to them. The method consists of comparing the records of blind rats with those of animals with intact sense organs. The possibility of vision was eliminated by the usual method of extirpation of the bulb. Three of the rats were subjected to an autopsy and a microscopical examination by Professor C. J. Herrick, who reports that all three were probably blind. Comparisons will be facilitated by certain classifications of the experiments.

1. The first group contains all those experiments in which no blind animals were tested, and hence comparisons are impossible. This group consists of the following experiments. Covering cage, covering maze, increase of illumination, decrease of illumination, rotation of a uniform environment, the second phase of uncovering the maze, and the 3rd, 4th, and 5th tests on rotating the maze.

2. The second group contains those experiments in which both seeing and blind animals were utilized but in which no rats were disturbed by the alterations. Obviously these experiments can furnish no data as to the function of vision. Nine blinds

were subjected to the "variable route" test and none were affected. Five blinds were tested on variations of method of handling without disturbing results. Two blinds were subjected to the first test on uncovering the maze and no effect was noticeable.

3. In the third class fall those experiments in which both blind and seeing rats were tested, but in which the disturbance was limited to those animals with vision.

Alterations in the position of the experimenter affected none of the five blind animals tested, while every member of a group of six normal rats was disturbed.

A change in the position of the maze had no effect upon any member of a group of five blind animals. In a group of six normal rats, four were affected and these made an average error record of 2.08.

4. In the remaining experiments, both blind and normal animals were tested and both groups were disturbed. The comparative records will need to be stated in detail for each experiment.

Degree of Hunger. Two blind rats were compared with ten normals. All members of both groups were disturbed. The blinds made errors the more frequently; the percentages of trials with error being 42 and 34 respectively for the blind and visual groups. The average error records for the two groups were 9.75 and 2.38 for the blinds and normals respectively. The blinds manifested their maximum of disturbance on the third trial while the normals gave the largest error record on the fifth trial. The blinds also exhibited the greater error record on a return to normal conditions.

Cleansing Maze. Seven blinds were compared with ten normals. Fewer blinds were affected, the percentages being 57 and 80. They made errors in 75% of their trials as compared with 61% for the normals. Their average error record was 6.00 as compared with 1.70 for the normals. Their greatest disturbance occurred on the first trial while the normals made their poorest record on the second trial. The time necessary to effect an adaptation was the same for the two groups. The blind animals exhibited the greater range of variability as to number of errors per rat; the average and the average variation for the blinds were 24.0 and 18.6 respectively, while the corresponding values for the normals were 10 and 5.6. The average variation relative to the size of the errors is thus much greater for the blind group.

Position of Cage.—Both groups contained ten rats. A smaller percentage of the blinds was affected, the values being 40 and 70. Those blinds affected were disturbed in a greater percentage of their trials (50 vs. 41), and made the greater average error score (1.33 vs. .87). The blind animals require a longer duration of exposure to induce an effect; they were disturbed only for the 24-hr. exposures, while the normals were affected by a 15-min. exposure. The blind rats also possessed the poorer adaptive power, for the normals became so accustomed to the novel situation in 24 hours that a disturbance was no longer manifest.

Rotation of Maze. Two blinds were tested on the first type of maze rotation, in which the three positions were tested on successive days. Their records are to be compared with those of ten normals. All members of both groups were disturbed. The blinds made errors in a greater percentage of their trials (67 vs. 65), but their average error record was much smaller (3.33 vs. 6.95). With a repetition of the test the poorer adaptive ability was manifested by the animals without vision; they decreased the percentage of trials in which error was present from 67 to 58, and their error record from 3.33 to 2.50. The visual group on the contrary reduced their error record from 6.95 to 1.72 and the percentage of runs with error from 65 to 47.

Rotation of Heterogeneous Maze Environment. The records of fourteen blind animals are to be compared with those of seven normal rats. A greater percentage of blind rats was disturbed (78 vs. 71). The errors of the blind group were confined to a smaller percentage of the trials (38 vs. 83). The blinds gave the larger error score (2.32 vs. 1.90) in spite of the fact that the errors were limited to fewer trials. The discrepancy is much greater when we compare the total number of errors per rat (18 vs. 12). The blinds exhibited the greater range of variability as to number of errors per rat; for the blinds the errors ranged from 3 to 70 with a mean variation of 15. The range for the normals was 9 to 15 with a mean variation of 2.2. The normal rats appeared to react definitely to the altered conditions. With each new change of conditions the errors were made at those places in the maze where the lighting conditions were altered the most. The blind animals, on the contrary, gave no evidence of reacting specifically to any observable changes. The errors were likely to occur anywhere within the maze. When the experiment was first performed, a group of four blinds was employed mainly as a control as no disturbance was expected. Since the number of errors was increased beyond the normal records, the test was repeated upon two other groups of blinds consisting of five each. The same results were obtained; the rats did not seem to be reacting to any specific feature in the environment and yet the normal number of errors was increased; some rats occasionally became almost hopelessly confused. Five animals made over 17 errors in a single trial.

Rotation of Maze and Environment. The records of five blinds are to be compared with those of ten normals. Eighty per cent of each group was disturbed. The blind animals made errors the more frequently, the percentage of runs with error being 42 and 31. The average error records of the blinds and normals were 7.76 and 1.29 respectively. The blinds exhibited the greater range of individual variability; the individual number of errors ranged between 3 and 172 for the blind rats and between 2 and 22 for the normals. The test was not repeated for the blinds so that comparisons as to adaptability are impossible. The blind rats, however, exhibited more disturbance after a return to normal conditions.

Rotation of Cage. Nine blind rats were tested. For the 15-min. exposure, all were affected, errors were present in 57% of the trials, and the average error record was 1.90. For the 24-hr. exposure, 90% were disturbed, errors were present in 62% of the trials, and the average error record was 4.95. A repetition of the tests disclosed no tendency toward adaptation.

Blind rats are more susceptible to these alterations than are the normals; blinds were disturbed by the 15-min. exposure while the normals were not. The blinds were also affected more by the 24-hr. shifts than were animals with vision. The blinds exhibited the greater range of individual variability as to number of errors, and the lesser powers of adaptability.

5. We are also able to compare the records of blind and normal animals in the mastery of the maze problem.

Vision aids untrained rats in learning a stationary maze, decreasing the number of trials by 28% and the total number of errors by 27%. The following records were obtained for 19 blind animals. The average number of trials involved in learning was 25. A perfect record was secured for the various groups on the 30th trial. An average total of 229 errors was made by each rat. The corresponding values for 27 normal animals were 18, 22, and 144. The generalization that vision may aid in the mastery of a stationary maze contradicts the findings of Watson in his study of kinaesthetic sensitivity. I do not question these results but doubt their universality. In these experiments the records of many blind rats and the average records of many groups of blind animals do not suffer in a comparison with the records of normal animals. One of the blind rats mastered the maze more quickly than any of the 27 normals. Two of the blind groups gave as good records as those of three groups of normals. On the other hand, six of the nineteen blinds did worse than the poorest of the 27 normals, and two groups of blinds gave a higher average record than the poorest group among the normals. While some individuals and some groups of blind animals do as well or better than the average run of the normal animals, yet there are many blind rats that do considerably worse than the majority of the normals. When the groups compared are rather large, there is likely to be a number of blind rats with extremely poor records and these cases are responsible for the poor group average. The blind rats exhibit the greater range of individual variability in their capacity to learn.

Vision aids trained rats to learn the rotated maze, decreasing the values by 35-40%. A group of 10 normals learned the rotated maze in 21.5 trials with an average total error score of 110. The corresponding values for three blind animals were 33.3 and 190. The rats had previously been trained on an alternation problem. The size of the blind group is too small, however, for a confident conclusion.

Vision is a detriment with untrained rats in mastering a rotated maze, increasing both number of trials and total errors. A group of six blinds learned the maze in 27 trials with an average error score of 117. The corresponding values for 10 normal rats were 30 and 196.

6. There are certain other peculiarities of blind rats con-

nected with their greater variability and erraticness. Blind rats are rather difficult to keep in good physical condition. They are more inclined to sluggishness in behavior, their appetite is frequently diminished, their hair becomes dry and rough, and they are sometimes rather flabby and cold to the touch. I have also noted what may be termed as a "breakdown," of which a number of examples may be cited. A group of six normals had been employed for four months in a sound discrimination experiment. Their conduct was normal and their physical condition was excellent at the conclusion of the experiment. These animals were now blinded and given the maze problem. Four of these rats proceeded to learn the maze in a normal manner for a number of trials and then suffered the "breakdown." They made complete failures of their attempts, became exhausted before success was achieved, and finally refused to run when placed in the maze. The break came on suddenly and occurred between the 6th and the 15th trials,—after the maze had been pretty well mastered. In another group of four animals without previous experience, one rat made rapid progress up to the 12th trial and then refused to run. The breakdown may occur at almost any stage of the experimentation. I had one individual that refused to run in the first trial. Another rat broke down on the 142nd trial during the control tests,—long after the maze had been mastered. Sometimes the rats simply quit and refuse to work further. Others work industriously but fail to find the food box, and are finally forced to cease their efforts through exhaustion; this behavior may be repeated in a number of successive trials until the rat quits and refuses to work when placed in the maze. Recovery from these breakdowns is rare and the rats may as well be eliminated from the experiment. I have tested such rats for a number of days in succession, and once a week for a couple of months in the hope that an interval of rest would induce recovery. These animals may continue to live and enjoy the average of health for blind rats. Some have been kept in the laboratory for five to six months. I have had some females bear and rear young subsequent to the breakdown. The phenomenon needs extended and systematic study.

The above differences in the comparative data obviously must be explained and interpreted in terms of vision. Certain conclusions can be asserted with confidence. Some interpretations must be regarded as suggestive.

Vision has a sensitive function. This statement means that the various objective alterations sometimes affected the animal's behavior through the medium of vision; in ordinary language we would say that the changes were perceived through the eye. The sensitivity of the eye is sufficiently proven by the third class of experiments in which the disturbances were limited to those animals with vision. Obviously these alterations were sensed wholly through the eye.

Most of these alterations may be sensed entirely through some other sense avenue than vision. The novel sensory conditions in the hunger experiment were obviously intraorganic in character. Vision can hardly be concerned in a sensitive way. In most of the experiments, the blind animals were affected; these blind animals must have sensed the novel conditions by means of other sense avenues than vision.

The normal animals probably utilized both of the above sensory means in reacting to the novel features in the fourth class of experiments. They possess both sensory capacities. The alteration can be perceived through this other sense modality since the blinds were affected. The alterations certainly possessed optical features. The differential sensitivity of blind and normal rats indicates that these changes were sensed wholly or in part through vision. The normal rats exhibited the greater degree of susceptibility or sensitivity to the alterations. The percentage of animals affected among the normals was equal to or greater than that for the blind rats with the exception of one experiment,—rotation of the cage. Obviously, this exception can not be explained on the hypothesis that the blind rats possessed modes of sensitivity not belonging to normal animals: it can be explained, however, in terms of principles to be developed later.

Vision possesses a corrective and adaptive function. The presence of eyes in some way increases the ability of the animal to adapt to these changes. Normal animals resist and overcome the disturbances better than do the blinds. The effect of this function is found in the greater rapidity of adaptation, a smaller error record, and a larger percentage of perfect runs. The best illustration of the operation of this function is found in the hunger experiment. Both groups of animals reacted to these alterations through a common mode of sensitivity and the percentage affected was the same for both groups. Vision, however, operated to minimize and overcome the effects of the disturbing conditions. The normal animals were able to make more perfect runs; they were able to resist the distracting influences more frequently than the blind rats. When disturbances did occur, the normal animals made by far the fewer errors; vision decreased the number of errors. Animals with vision exhibited the greater tendency to adapt themselves to these novel situations; they also recuperated from the effects more quickly after a return to normal conditions. Comparing the records of the two groups in the various experiments of the fourth class, we find that the adaptive and recuperative power of the normals is equal to or greater than that of the blind animals in every case. The normal animals made a greater percentage of perfect runs with the exception of one experiment; evidently they are more able to resist the distractive conditions. Rats with vision gave the smaller error score in every experiment but one; they thus possess the power of minimizing the disturbance when it occurs. When comparisons are possible as to the correlation between the maximum disturbance and the duration of exposure to the novel conditions, we find that the normal animals are the more resistant in three of four cases. The blind rats invariably exhibit the greater variability as to the range of errors. Blind rats are extremely variable as to number of errors; they are more likely to go to pieces, become lost and run high error scores when they are disturbed; this fact would indicate that vision operates as a corrective and control.

The discrepancies and exceptions in the application of the above two principles of explanation become explicable when we consider that the two functions of sensitivity and adaptation are antagonistic in their effects. The greater the sensitivity the larger will be the number of animals affected, the percentage of runs with error, and the total number of errors. The corrective function will operate to decrease the number of errors and the percentage of runs with error; it might also decrease the number of animals susceptible to the disturbing changes. The two functions, although antagonistic in their effects, are not necessarily mutually exclusive; both may conceivably operate at the same time. The actual records secured in any experiment will thus be a function of the relative strength of the two tendencies. In one type of situation the sensitive function may be the more effective in determining the character of the records, while the adaptive function may be the more efficacious in another experimental situation. The two experiments which deviated from the usual rule were rotation of maze and rotation of cage. The average error score of the normals was less than that of the blinds with the exception of the maze rotation experiment. We have here a rotation in reference to a predominantly optical situation, and one would expect that the sensitive function of the eye would predominate in effectiveness; the disturbance is so great that the corrective effects are not sufficient to reduce the error record below that of the blind animals. When the test was repeated, we find that the normal groups made the greater adaptive progress, and reduced their error score below that of the blinds. When the corrective function is given time to become efficacious, the error records no longer constitute an exception to the rule. When the cage was rotated, normal animals were not affected by a 15-min. exposure, while the blind rats were. We may explain this difference in susceptibility on the hypothesis that the corrective function of vision enabled the normal animals to resist the disturbing effects of the new conditions. With a 24-hr. exposure both groups were affected, but the blinds manifested the greater disturbance and the normals exhibited the greater tendency toward adaptation. The normal rats thus were no longer able to resist the cumulative effects of a prolonged exposure, but the corrective function of vision enabled them to reduce the degree of the disturbance and hasten adaptation.

The corrective and sensitive functions of vision are also evident from a comparison of the records of normal rats in the different experiments. When the maze was rotated in reference to a stationary heterogeneous environment, the normal animals were exceedingly disturbed but they made marked progress in adaptation when the test was repeated. A rotation of the maze and a uniform optical environment gave a lesser degree of disturbance and no tendency toward adaptation. The difference in the two alterations was presumably optical in the main. The greater the optical changes, the greater was the sensitivity and the adaptive power of the animals. Likewise, when normal rats were rotated in an open and a covered cage, the greater sensitivity was manifested in the former case. Many similar illustrations can be given.

The terms "sensitive" and "corrective" have so far been used in a purely descriptive sense, to state certain differences of fact. As explanatory concepts they render but little service.

In attempting to explain the greater sensitivity of the normal rats to all alterations instituted after the mastery of the maze, two possibilities exist; these functions of vision we may term "directive" and "distractive." The first hypothesis assumes that the motor activity of the animal is guided and directed in part by the visual impulses released by the stimuli from the objective environment. When the relation between the rat and these features of the environment is altered, motor disturbances are the inevitable result. It is possible that this directive function of vision may be present during the mastery of the maze but absent after the act has been thoroughly developed. The distractive hypothesis assumes that the maze habit is influenced in no way by the visual environment so long as it remains stable. Any pronounced alteration, however, is sensed immediately and operates as a distractive stimulus; in common parlance, it attracts the animal's attention, the rat reacts to the new conditions, and as a consequence the maze habit is disrupted. These two functions are not necessarily mutually exclusive; it is possible that both may be efficacious in mediating the disturbance in any run through the maze.

Between the two explanatory conceptions, we are forced to conclude in favor of the distraction hypothesis as far as the normal animals are concerned. When the position of the experimenter was altered, the rats were never disturbed in that section of the maze near which the experimenter had been standing. In fact the animals were not disturbed at any position in the maze at which they were oriented towards the old position of the experimenter. This fact would indicate that the rats did not employ visual stimuli from this source in any effective fashion in directing and orienting their conduct in the maze. The disturbance did occur, however, in those sections of the maze near the new position of the experimenter and when the rats were oriented in his direction. When the animals left the true pathway, they invariably ran towards the experimenter. This positive reaction can not be considered a directive habit acquired in learning the maze because the conformation of the maze at the old position was such as to prevent it. The positive reaction can better be regarded as a feeding habit developed in the living cage and on the feeding table. The experimenter thus attracted the animal's attention because of the novelty of the position and stimulated an old habit acquired while the rat was being handled and fed. The arousal of this habit naturally disrupted the normal functioning of the maze act. In several experiments such as increasing and decreasing the illumination, rotating the maze in darkened and lighted environments, and rotating a heterogeneous environment, the following behavior was frequently noted: Animals suffered a pronounced disturbance at those points where the illumination had been greatly increased. I have frequently seen animals run the maze without error up to a point where an alley, customarily darkened, was flooded with a beam of strong daylight. Here the rat stopped suddenly, exhibited strong signs of nervousness and timidity with frequent retracing in search of another path. Decreasing the illumination in any part of the maze seemed to be without effect, but a pronounced increase was effective. These facts indicate that the alterations served as distractions. The distractive theory is further supported by the irregular and occasional character of the disturbances. This feature of the results was summarized in the first paper. It refers to such facts that many trials are without error, that rats are immune in one experiment and susceptible in another, and that the number of errors made in various trials is extremely variable. If the rats are relying upon the objective data to guide their conduct in the maze, it would seem that any rat should be disturbed in every trial until complete adaptation is secured. The fact that the disturbances occur in a perfectly haphazard and accidental manner is readily interpreted on the basis of the distractive theory. The disturbance is present only when the alterations attract the attention of the rat, and this result is largely a matter of chance. Conclusive proof of the distractive function is obtained from the comparative records on covering and uncovering the maze. Rats learned the uncovered maze,—a maze with a well lighted and heterogeneous optical environment. The maze is now covered with the canvas top. A uniform but darkened environment is substituted for that present while the maze was mastered. If the rat is relying upon these visual objects as directive stimuli in threading the maze, their sudden removal should disrupt the act. No animals were disturbed in this test, and we are forced to conclude that vision possessed no directive function after the maze was mastered. We may also assume that the alteration did not operate as a distraction because the new environment was homogeneous and poorly lighted. In the opposite experiment of uncovering the maze, we may conclude that vision of the extraneous environment possessed no directive function because the conditions were such that no possibilities were present for its development. The maze was mastered in a homogeneous optical environment. Removal of the top and the introduction of a well illumined and heterogeneous environment resulted in disturbances. Evidently these novel conditions were effective only as distractions. If we could generalize from these experiments, we would be forced to conclude that all disturbances due to alterations after the maze is learned and while the rat is running are the result of distractions.

There is but one possible exception to the above formulation,—certain characteristics of behavior when the sideless maze was rotated. After rotation the animals frequently drifted to that corner at which the food box had formerly been located. This fact would indicate that the rats can orient themselves in reference to the position of the food box in terms of stimuli emanating from the extraneous environment. The same behavior was occasionally noted in the rotation of the standard maze when the extraneous environment near the food box possessed unusual features, as an open window giving good light. Granted that this fact indicates a directive function, yet it is by no means certain that it was mediated through vision rather than smell or some other sense, for no blind animals were employed as controls in this experiment. The fact can be interpreted, however, in terms of the distractive function. It is possible that certain unusual features in the environment near the position of the food box operated as a distractive stimulus and that the rats reacted to it in a positive manner. We may then safely conclude that alterations instituted after the maze is mastered and while it is being run may and do operate as distractive stimuli in so far as they are sensed through vision; it is also possible that certain alterations may disturb the animal because these stimuli had been utilized as guides in running the maze, but no affirmative statements can be made with confidence.

Blind animals were also disturbed and this disturbance was mediated through other senses than vision; we must also assume that normal animals were disturbed in part through other modalities of sense than vision. This disturbance may also be explained by the assumption that these other senses were susceptible to the altered conditions either as distractions or as motor controls. There are no facts which support the directive hypothesis in a conclusive fashion. Certain facts can hardly be interpreted in other than distractive terms. The effect of varying the degree of hunger is obvious. The haphazard and occasional character of the disturbance was more characteristic of the behavior of the blind than of the normal animals, and this fact is best explained by the distractive hypothesis. The differential sensitivity of the normal and blind rats is thus one of degree and not of kind. Normal animals manifest the greater degree of susceptibility to the changes because they are affected through more sensory avenues.

The comparative learning records of the various groups of animals furnish certain data relative to the function of vision.

1. Normal rats master a stationary maze more readily than a rotated maze, and an open maze quicker than a covered one. These facts can be explained in terms of either the distractive or directive hypotheses. If the animal can utilize objective stimuli as guides or controls, the presence and stability of an optical environment should facilitate the learning process. Likewise these objective stimuli may function merely to attract the animal's attention, encourage unnecessary and disadvantageous excursions, and otherwise distract the animal from the more serious business at hand. On this hypothesis a changing environment would operate as a more effective distractor than a stationary one. Likewise, the distractive effect of a heterogeneous environment would be greater than that of a uniform one.

2. Rats with vision learn a stationary maze more easily than do blind animals. This poorer learning capacity of blind rats may be explained in numerous ways: a. We may assume that

the normal animals learn to utilize visual stimuli as controls in selecting the true path from the numerous *cul de sacs*. b. Vision may be advantageous because of the tonic effect of light. Visual stimuli exert a tonic and stimulative effect upon the various activities of the organism. Rats with vision exhibit the greater vigor and superabundance of bodily activity. Surplus activity is necessarily valuable in any trial and error mode of learning. This effect of light will also be manifested by the vital activities. Heightened vitality will be influential via of an increased retentive capacity or a stronger hunger motive. Decreased activity and vitality resulting from loss of vision may interact upon each other; decreased activity, or lack of exercise, will lower the vital tonus of the organism, and this lowered vitality will in turn produce sluggishness of behavior. c. We may assume that the learning capacity of blind rats has been minimized by certain deleterious effects of the operation per se. The connection between these effects and learning capacity may be conceived in several ways. The operation (the surgical shock or the effect of the ether) may act directly upon the vital activities and thus influence learning capacity as sketched above. The organic aftereffects may be conceived as some sort of a nervous irritant which operates as a distractive stimulus and thus produces erratic and exaggerated behavior. Likewise the effects may be nervous modifications of such a character as to render the animal more susceptible than usual to any novel stimulative conditions. The animal is thus prone to erratic, irregular and exaggerated modes of response detrimental to the mastery of the maze. On this hypothesis, stability and instability will characterize normal and blind rats respectively.

The last two hypotheses are supported by several lines of evidence. Blind rats frequently exhibit signs of decreased vitality such as muscular flabbiness, rough coats, poor circulation, poor appetite, and a susceptibility to disease. Blind animals are also less active as a general rule; the normal vigor, persistence, and superabundance of activity is frequently lacking. The phenomenon of breakdowns characteristic of blind rats also suggests the validity of the third conception. The greater erraticness and variability of blind animals,—the tendency to make now and then unusually large error scores, is explicable in terms of the third conception. There are no facts which directly support the first conception of a directive function of vision.

3. Vision is a detriment to the mastery of the rotated maze when untrained animals are utilized. This fact cannot be explained on the assumption that rotation is detrimental because visual-motor habits are continually being disrupted, because rotation will prevent the development of any such visual habits. Only one possibility remains,—the assumption that these visual alterations operate as distractions.

4. Vision is an advantage in the mastery of the maze, when the rats have had previous experience on other problems. The paucity of data upon which this conclusion is based renders its validity questionable. Accepting the fact at its face value, we may assume that the previous experience of the normal animals has operated to render them less dependent upon the extraneous environment; this result will minimize their susceptibility to the distractive influences of the rotation as demanded by the conclusion of the previous paragraph. The two groups thus approximate equality as to susceptibility to the distractions due to rotation, and the visual group is now enabled to master the maze more readily in virtue of its greater learning capacity.

All comparative data on the mastery of the maze can thus be explained on the assumption that vision possesses both detrimental and beneficial features in relation to the mastery of a maze problem. Visual stimuli tend to distract the animal and thus retard the development of the kinaesthetic-motor habit. The existence of vision on the other hand increases learning capacity. Two conceptions of the relation between vision and learning capacity receive some factual support. Light exerts a tonic and stimulative effect upon activity, while on the other hand the removal of the eye balls is to be regarded as some sort of a positive disturbing or distracting factor.

As to the nature of the process of adaptation, certain explanatory conceptions may be suggested. 1. We may suppose that the alterations disrupt the system of sensori-motor connections involved in running the maze, and that adaptation is to be conceived as a process of reorganization,—the acquisition of new motor controls. This conception assumes a directive function for the senses involved. Animals with vision have an advantage because they can utilize visual as well as other sensory cues.

2. The distractions and resulting errors induce confusion and excitement, and this confusion may now operate as a further distraction. Adaptation is a process of minimizing and allaying this excitement, and all familiar or unaltered stimuli will possess this quieting and reassuring characteristic. Adaptation is a matter of learning to direct the attention to the familiar aspects of the environment. Rats with vision will have an advantage because of their greater learning capacity and their greater sensory contact with the environment. 3. The disturbances are due to distracting stimuli, and adaptation is a process of strengthening the maze habit up to a point where it is immune to the distractive effects of those particular stimuli. Adaptation is thus a further process of learning, and those animals with the greater learning capacity will manifest the greater adaptive power. On this assumption the adaptive capacity of normal rats will be greater than that belonging to blind animals. 4. Blind rats are less resistant to distractions because of the operative effects. As previously noted, these effects may be conceived as intraorganic distractive stimuli of some sort, or as nervous conditions conducing to exaggerated and erratic responses. Blind rats will be regarded as essentially unstable organisms, subnormal in their capacity of resisting distracting stimuli. 5. Adaptation may be conceived as a process of decreasing sensory susceptibility to stimuli due to neural or end organ changes somewhat akin to fatigue. On this hypothesis any end organ can adapt only to those alterations which were sensed by that receptor.

The factual data are insufficient for any very confident judgments as to the relative validity of these various hypotheses. The normal animals manifested by far the greater adaptive power; this fact is readily explicable in terms of any one of the first four conceptions. The difference of adaptive capacity of the two groups is generally greater than their differences in learning ability as manifested in the mastery of the maze; this fact militates against the 1st and 3rd conceptions as complete explanations of adaptation. The first conception must be summarily dismissed as the facts indicate rather conclusively that extraneous stimuli do not function as motor controls after the maze is mastered. The greater variability of the blind rats may be explained on the basis of either the 2nd or the 4th hypotheses. The immunity to distractions due to adaptation is mainly specific rather than general; this fact eliminates the 3rd hypothesis as a complete explanation of the process, since rats in time should become practically immune to all ordinary distractions. Neither can the fact be readily envisaged under the 4th and 5th conceptions; it is most easily explicable in terms of the 2nd hypothesis. A sense organ can play a part in the process of adaptation although the disturbance was mediated through some other sense avenue. Normal rats displayed the greater adaptive power in the hunger experiment, so that vision must have been concerned in the process although the disturbing conditions were intraorganic. This fact would eliminate the 5th conception as a complete explanation of adaptation. The maximum adaptive power of normal rats was manifested in those experiments in which the optical features of the environment were altered. Adaptation was very rapid when either the maze or the environment was rotated in reference to each other, but no adaptation was present when both maze and environment were rotated simultaneously. This fact may be conceived in either of two ways: 1. We may assume that the eye can adapt only for visual distractions. This assumption naturally suggests the 5th conception. 2. We may assume the truth of the 2nd conception, and explain the inability of the normal rats to adapt to the rotation of maze and environment as due to the homogeneity of the visual environment in this experiment.

These conceptions are not mutually exclusive; all may contribute to the process of adaptation. Only the first possibility must be summarily dismissed. The second conception receives the most support, as there are no facts which can not be explained in its terms. The 3rd conception meets the greatest amount of difficulty; it can not account for the entire process of adaptation. The evidence for and against the 5th hypothesis is about equally balanced.

CONCLUSIONS

The white rat is sensitive to optical stimuli through the medium of the eye.

Both advantages and disadvantages accrue from the possession of visual receptors in the maze situation.

Vision is detrimental because of the distractive effect of retinal stimuli.

The advantageous features of vision may be explained in either of two ways: Retinal stimuli exert a tonic and stimulative effect upon organic activities and thus promote learning capacity, or one may assume that blind animals are at a disadvantage because of certain deleterious effects of the operation.

Vision may possess other functions in the maze situation; our facts are inconclusive on many points.

These conclusions apply merely to the situations obtaining in our experiments; other potentialities of vision may be realized in different types of situation.

MAZE STUDIES WITH THE WHITE RAT

III. Anosmic Animals

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Anosmic animals were employed to determine the function of olfaction in the environmental alterations described in the first paper. Records were secured from nine anosmic and five blind and anosmic rats. For these animals I am indebted to Miss Vincent. Professor Herrick made a histological examination of a group of seven of these defective rats. He reported that the operation was successful for two of the anosmic animals and for but one of the five blind and anosmics. From this record it is obvious that no conclusions drawn from the records of defective animals can be trusted without a subsequent histological examination. In our comparisons we shall utilize the data from the three animals of whose defective condition we are certain. Any conclusions from such a small group must necessarily be regarded with suspicion; however, we shall state the facts as they are and indicate their significance.

ANOSMIC ANIMALS

The anosmic operation exhibited no apparent deleterious effect upon the vitality of the animals. These animals were kept in the laboratory for nearly a year. Their appetite was undiminished; they looked sleek and well groomed, and the vigor and abundance of their activity was equal to that of normal animals.

One of the anosmic animals mastered the standard maze in two trials with a total error score of 40. The other rat required 21 trials and 127 errors to master the same maze. The average values for a group of 27 normal rats in mastering this maze were 18 trials and 144 errors. Evidently smell is not essential to the mastery of this type of maze. In this connection the construction of this maze must be considered; it was nearly water-tight and covered with closely fitting glass covers. Any olfactory contact with the extraneous environment must have been greatly minimized.

In the cleanliness test a single error was made by one animal in the first trial. A pronounced disturbance was manifested by members of the normal and blind groups of animals. Presumably, the alterations in this experiment were primarily olfactory in character. The facts indicate that these novel disturbing conditions are sensed wholly or mainly by means of smell.

The maze was learned with one side of the top open. This top was now removed. No disturbance resulted; neither were normal animals affected.

Both animals were affected by the rotation of the heterogeneous environment. Their average error record was 2.50 and errors were present in 75% of the trials. The disturbing effect was practically eliminated when the test was repeated. The average error score per rat for the first test was 15. These results are similar to those obtained for normal animals.

Both animals were slightly disturbed when both maze and environment were rotated. The average error record was but .42 and the errors were confined to one-third of the trials. The adaptive capacity of this group was not tested. These results are similar to those for normal animals with the exception of a smaller error score. Taken at their face value, the facts indicate that anosmic animals are less sensitive to these changes than are normal or blind rats.

Rotation of the uncovered maze disturbed both animals. Their error record for the first test was 5.08, and the disturbance was present in 83% of the trials. A repetition of the test reduced the above values to 1.00 and 60% respectively. For the first test the normal records were 6.95 and 65%, while the corresponding values for the second test were 1.72 and 47%. These results indicate that anosmic animals are slightly less sensitive to these changes than are normal rats.

Variations in the position of the living cage exerted a pronounced disturbance with one rat and a slight disturbance with the other. The average error record was 5.00 and errors were present in 75% of the trials. These rats were subjected to a 24-hr. exposure before being tested. The results indicate a greater susceptibility than that of either blind or normal animals; a corrective function must be ascribed to olfaction in this case.

The cage was first rotated for the three new positions on successive days. No disturbance was manifested. Both blinds and normals were disturbed in similar conditions. This fact would indicate a sensitive function for olfaction. The rats were now left in each new position for five days and tested daily. No effect was observable for the first position. In the second position both rats manifested considerable hesitancy and indecision in nearly every run and one rat made eleven errors in one trial. The hesitancy and indecision were again apparent for the third position; one rat made fourteen errors in two trials, and the other eleven errors in one trial. Prolonged exposure thus induces a disturbance. The fact again indicates a defective sensitivity on the part of these rats.

These two anosmic rats belonged to a group of three animals, one of which died before the series of tests were completed. The record of this rat which was not histologically examined was similar in every respect to those given above.

A group of six anosmics were subjected to several tests on the sideless maze in the early part of the experimentation; these were not examined. Their results, however, were similar to those two which are known to be anosmic. The degree of disturbance was practically identical with that for normal rats in the following experiments,—position of experimenter, position of maze, and rotation of maze. They exhibited little evidence of any disturbance when the cage was rotated or altered in position.

BLIND AND ANOSMIC ANIMALS

Five such animals were tested and afterwards examined. All were pronounced blind. The anosmic operation was completely successful in but one case. Both olfactory bulbs were intact with one animal; evidently the bulbulous material in front of the olfactory lobes had been removed in this animal. With two animals the left lobe had been successfully removed while the right lobe remained intact or partly severed. In the remaining animal the sections were made through the frontal lobes of the cerebral hemisphere; on one side the section was sufficient to destroy olfaction; on the other olfactory connections were still possible. This group of rats thus consists of one blind, one blind and anosmic, two blind and partially anosmic, and one which we may term a defective because of the loss of considerable cerebral tissue.

The learning records of this group of animals present many interesting features. The blind animal mastered the maze in 24 trials with a total error score of 152. After this time, the rat ran the maze consistently without error. This record is similar to those for blind and normal animals. Those two that were blind, and anosmic on the left side gave poorer records; one required 52 trials and 144 errors, and the second 102 trials and 508 errors. After the maze was mastered according to the criterion used, many errors kept appearing in an irregular manner for 25 to 40 trials. The blind and anosmic animal did still poorer; it required 130 trials and 2582 errors to learn this maze, but the act did not become thoroughly automatic until the 200th trial. It was also necessary to help this rat in 76 trials while learning the maze. In the early trials this animal utterly failed to reach the food box after several hours of effort and an error score of over 100. After the animal became exhausted I would stimulate it to further efforts and guide it when necessary. After the twentieth run I aided the rat whenever it became apparent that it was hopelessly lost. The defective rat required 194 trials and 1855 errors to master the maze. It was also helped in 32 of its trials. The act did not become thoroughly automatized for some time after the maze was considered learned. These results are significant because the difficulty of mastery is proportional to the degree of olfactory deficiency. The loss of either smell or vision does not operate as a detriment to the mastery of the maze; the loss of vision together with the partial or total destruction of smell is exceedingly detrimental. Evidently the deficiency due to the absence of either vision or smell is compensated in some manner by the other sense, while the remaining senses are unable to compensate for the deficiencies of both.

Rotation of the heterogeneous environment produced little disturbance upon the blind and anosmic or upon those which were blind and partially anosmic. The average error records for six trials were .33 and .66 respectively. The error record of the defective animal was 2.33. The normals gave a score of 1.90, the blinds 2.32, and the anosmics 2.50. Evidently the loss of both senses minimizes or practically abolishes the rat's sensitivity to these changes.

Uncovering the maze produced no effect. Neither was a disturbance manifested by the normals or the anosmics.

In the cleanliness test the blind and anosmic made 14 errors in one of its trials. Those which were blind and partially anosmic gave an error record of .50. These animals exhibited about the same degree of sensitivity as the anosmics. Their sensitivity was much less than that of either the normals or blinds.

Only one blind and partially anosmic animal was subjected to a rotation of maze and environment; its error record for six trials was 4.16, which is greater than those for normals or anosmics, but less than that for the blind rats.

The blind and anosmic was not affected by a rotation of the maze. A blind and partially anosmic rat gave an error score of 2.50, which is less than that for either anosmics, normals or blinds.

The blind and anosmic animal was not affected by changes in the position of the maze. The two which were blind and partially anosmic gave an error record of .75 which is less than that for any of the other sensory groups.

The blind and anosmic rat was disturbed by a rotation of the cage only after a considerable period of exposure to the novel situation. Errors were present in three of fourteen trials. The average error record was .78. The degree of sensitivity was about the same as that for the anosmics. The two blind and partially anosmic animals were more susceptible; their error record was 1.68 for eighteen trials. These animals were disturbed less than either the blind or normal groups.

A significant feature of these results is the practical insensitivity of the blind and anosmic rat to all alterations instituted after the mastery of the maze. A total of 50 trials was given, of which 80% were without error. The average error record for the 50 trials was 1.50. In the previous 50 runs, errors were absent in but 59% of the trials and the average error record was 2.70. This animal made a better record during the tests than during the later stages of increasing automaticity and after the maze was considered mastered. No errors were present in the first four experiments involving a total of 24 trials. The first indication of a disturbance was manifested in the fifth experiment in which the cage was rotated; a total of 11 errors was made in three of the 14 trials. The sixth test involved the cleansing of the maze, and 14 errors occurred in the first trial. After the regular series of tests were completed, both cage and maze were rotated simultaneously in the hope of inducing more serious effects; error scores of 40, 5, and 1 were secured in three of the 10 trials. Rotation of cage and cleansing the maze were the only tests which induced disturbances, and it is possible that these results may have been due to chance irregularities. Granted the validity of the results, the question arises as to the sense avenue through which the changes were instituted. The changes resulting from cleansing the maze may well have been perceived through the sense of contact, for undoubtedly the contact values of the bottom of the runways were altered. Rotation of the cage may have affected the animal by means of its sensitivity to heat as the cage was located in the proximity of a steam radiator.

The practical insensitivity of the blind and anosmic animal considered in conjunction with the sensitivity of all other groups including those animals which were blind and partially anosmic indicates that all of these alterations are sensed almost wholly through smell and vision. This conclusion does not warrant the assumption that the rat does not possess any other efficient avenues of sensitivity. The statement merely means that smell and vision are the only senses adapted to the detection of these particular alterations of the environment.

Since vision and smell are the only effective senses in our conditions, it follows that all disturbances manifested by the anosmic group must have been instituted by means of vision, and that we can utilize the data of this group in determining the function of vision. This hypothesis is supported by the facts, for the results are in harmony with the conclusions as to the function of vision previously derived from the differential records of the blind and normal animals. All experiments involving an alteration of the optical environment were very effective upon the anosmic animals; this group of tests comprised rotation of environment, rotation of uncovered maze, and a change in the position of the living cage. On the other hand those experiments involving a minimal optical element, such as cleansing the maze and rotation of the covered maze, had little effect upon this group of rats. Moreover, the anosmic group when disturbed exhibited powers of adaptability on a par with normal animals. This adaptive capacity was in evidence in the experiments in which the environment was rotated in reference to the maze, or the maze was rotated in relation to the environment. The records of these anosmic animals thus confirm our previous conclusion as to the sensitive and corrective values of vision.

The function of smell may be determined from several sources. 1. Since no other senses than smell and vision are concerned in these tests, the records of the blind rats must be due exclusively to the olfactory factor. 2. The differential sensitivity of the blinds as compared with those blind and partially anosmic must be interpreted in terms of smell. 3. The records of the normals as compared with those of the anosmic group must likewise be explained in terms of smell.

Smell possesses a sensitive function; by this statement we mean that these alterations do affect in some way the animal's behavior through the medium of olfaction. All three sets of facts support this conclusion. The blind and partially anosmic group suffered less disturbance than the blind rats in every experiment in which comparisons are possible. The anosmics on the whole manifested a lesser degree of sensitivity than did the normal animals; their sensitivity was much less for those experiments, e.g., cleanliness test, in which the olfactory element predominated. The blind animals, possessing only smell, exhibited the maximum amount of disturbance in those experiments in which the anosmic animals were the least sensitive. In the cleanliness test, those animals with smell intact,—blind and normal groups, suffered a pronounced disturbance, while but little effect was manifested by those groups in which olfaction was partly or completely eliminated.

In the previous paper, we noted that blind rats were sensitive to alterations of the environment, and concluded that these alterations operated as distractive stimuli rather than as motor controls. The results of this paper prove that smell is the main mediating sense involved in the detection of these changes by blind rats. No additional facts were developed necessitating a revision of the conclusion as to the distractive character of these olfactory stimuli.

Several significant features are contributed by the experiments concerning the functions of smell and vision in the mastery of the maze. Anosmic animals learn the maze as readily as do normal rats. The olfactory operation produces no deleterious effect upon the vitality or behavior of the animals. The elimination of vision slightly decreases learning capacity, but this effect is limited to certain individuals; the vital capacity of certain rats is also lowered. The combined loss of smell and vision exerts some effect upon vitality, but this effect is apparently no greater than that resulting from the loss of vision alone. The combined loss of the two senses results in a pronounced decrease in learning capacity, an effect which can not be regarded as the arithmetical sum of the results of the two operations taken separately.

These facts indicate that the diminished vitality and learning capacity of the blind animals and the blind and anosmic groups can not be due to any effects of the operation *per se*, such as surgical shock, ether effects, etc. The anosmic operation is much more serious and difficult than the optic one, and any operative effects should be more evident and more extensive in the anosmic than in the blind groups. The reverse situation obtained; the anosmics were not affected while many of the blind rats were. The combined operation for the two senses is not any more prolonged or severe than for smell alone. If the operative effects are responsible for the deficiencies of learning capacity, one should expect as good records from the blind and anosmic groups as from the anosmic animals; as a matter of fact the anosmic animals suffered no deleterious effects while the learning capacity of the blind and anosmic rats was far below normal.

In the previous paper we noted three possible ways in which any sense might function in order to increase learning capacity. Sensitivity may be advantageous because of either a directive or tonic influence upon behavior and the vital activities. The removal of a sense organ may be disadvantageous not because of the elimination of sensitivity but because of certain deleterious effects of the operation itself. The directive function of vision for our conditions was decisively eliminated as one of the possibilities. The data of this paper also eliminates the third hypothesis. We are thus forced to conclude that the beneficial influence of vision upon learning capacity is due to the tonic and stimulative effect of retinal stimuli.

Similar possibilities obtain for the function of smell in the acquisition of the maze habit. The facts previously given exclude the hypothesis of operative effects for smell as well as for vision. As between the directive and tonic hypotheses no confident decision can be made. The records of the blind rats indicate that smell exerts no directive function after the maze is learned, but it is possible that olfactory controls may be utilized in the formation of the habit and yet be noneffective after the maze is mastered. The functions of smell and vision compensate for each other in the learning process. This fact is most easily interpreted on the basis that both senses have the same function. Since vision is efficacious because of its tonic effect, we would need to assume the same function for smell. On this hypothesis, a certain amount of sensory stimulation is necessary to induce sufficient motor activity requisite for learning. This effect can be secured through either smell or vision, while the elimination of both senses is disastrous. However, it is not entirely impossible to conceive that the two senses may compensate for each other even though their functions are different. One may suppose that vision exerts a tonic effect while the function of smell is that of control. There is good evidence that control is secured mainly through the medium of the cutaneous and kinaesthetic senses. One may now suppose that the cutaneous and kinaesthetic control requires a certain amount of supplementation and that this effect may be furnished by either the tonic function of vision or the additional control exerted by smell. A final fact supports the tonic hypothesis for both smell and vision. The blind and anosmic animals differed from the other groups in that they lacked persistence, initiative and incentive. I refer to the fact that these animals required help or additional stimulation in many of their trials. One possible interpretation of this fact is obvious; we may assume that these animals lacked a sufficient amount of sensory stimulation to arouse the motor activity adequate to the situation. Their activity was deficient in vigor, decisiveness, and persistence. These animals possessed the normal amount of energy, and the proper kind of stimuli for the control and direction of this energy, but they were so deficient in their sensory capacity that an adequate amount of this potential energy was not released. Additional stimuli of an auditory or cutaneous character were requisite to overcome this deficiency.

The comparative data confirm our previous conclusion that the eye possesses some peculiar adaptive capacity. The adaptive power of anosmic animals is practically equal to that of the normals, while the capacity of both groups is much superior to that of the blind animals. The superiority of one group over another is thus not a matter of the number of senses, but rather of the kind of sense involved. Adaptation can not be conceived as a pure process of learning, since the blind and partially anosmic animals appeared to adapt as readily as did the blind rats although their learning capacity is much inferior. Neither can the differences in adaptive capacity of the various groups be due to operative effects, for on this hypothesis the adaptive ability of the anosmics should be inferior to that of the blind animals.

There is no conclusive evidence that smell is concerned in the process of adaptation. Although the blind rats did adapt to the distractive influences of olfactory alterations, it is entirely possible that this effect was mediated through the kinaesthetic-motor processes. There is some evidence that the distractions mediated through one sense can be corrected for through another. If smell is concerned in any overt manner in the process of adaptation, one would expect the adaptive power of normal animals to be greater than that of anosmic rats. Likewise blind rats should manifest greater ability than that possessed by blind and partially anosmic animals. There are no facts which indicate in any conclusive fashion the truth of either of these suppositions.

CONCLUSIONS

The results of this series of experiments confirm the conclusions of other investigators that the maze habit consists essentially of a tactual-kinaesthetic motor coordination.

This act is dependent, nevertheless, both during and subsequent to its development upon a wider sensory situation of which it is a part. This fact was proven by an experimental control of the relation between the animal and the environment.

The sensory connection between the act and those aspects of the environment which were altered was mediated almost exclusively through vision and smell.

The development of the act is contingent upon retinal impulses in two ways. On the one hand, retinal impulses operate as distractions, tending to prevent and delay the final perfection of the coordination. This distractive effect is present even when the relation of the visual environment to the rat remains stable. Any alteration of the environment from trial to trial increases the distractive effect. On the other hand, these retinal impulses tend to promote or condition the organization of the component elements of the act in so far as these impulses arouse the motor activity requisite to the solution of the problem. There are several ways of conceiving of this relation between visual stimuli and increased learning capacity. The experiment furnished no data for a choice between the several possibilities.

The development of the act is also dependent upon olfactory stimuli. No facts are pertinent as to the distractive or detrimental effect of these stimuli. Olfactory impulses, however, aid in the development of the act. These stimuli may be utilized as controls, or one may suppose that they are advantageous because of their tonic effect upon the various activities involved in the process of learning. No confident decision can be made as between these alternatives, though the latter hypothesis receives the greater support from the relevant data.

The act is still dependent upon these visual and olfactory stimuli after it has become thoroughly automatized, provided it was developed while these stimuli were present. The act can be acquired and function successfully when these stimuli have been completely eliminated. When the act was acquired while these stimuli were present, it will still function successfully when they are subtracted at least in part, or so long as their positional relations to the organism remain unaltered. Any positional change of these stimuli or the addition of new elements operate to disrupt or interfere temporarily with the successful functioning of the act. These changes of the stimuli function as distractions; they release impulses which the organism is unable to integrate successfully into the series of motor activities. The act is temporarily disrupted or disorganized.

Some degree of adaptation to these disturbances is the rule for all sensory groups. The experiments furnished no data which prove that smell is concerned in the process of adaptation. Vision certainly possesses an adaptive function. Of the five suggested hypotheses as to the relation between vision and adaptation, two are disproven by the experimental data. Three possibilities remain. Adaptation may be a further process of automatization and rats with vision are at an advantage because of their greater learning capacity. Adaptation can not be explained wholly in terms of this conception as the adaptive capacity of the various groups of animals is not proportional to their relative learning ability. Visual adaptation may be a process of decreasing sensory susceptibility to the distractive stimuli. This conception can not wholly explain the phenomenon as certain facts indicate that vision can correct for disturbances mediated through other sensory avenues. Unaltered or familiar visual stimuli exert a quieting and reassuring effect upon the organism and enable it to resist the distractive effects of other stimuli. There are no facts which can not be explained fairly successfully on the basis of this hypothesis.

The maze act and the learning process are much more complicated phenomena than the conclusions of some previous investigators would indicate. The habit does not consist merely of tactual, kinaesthetic and motor elements. Other accessory and conditioning components are also present. Learning does not consist merely of the organization of certain tactual and kinaesthetic stimuli with certain movements. Many other sensory factors are present which release their quota of impulses that must be harmoniously integrated and organized in some fashion adapted to the solution of the problem.

All statements as to the functions of smell, vision, or other senses must be interpreted as applying only to the situations obtaining in these experiments.

NOTES ON THE MIGRATION OF THE HESSIAN FLY LARVAE[1]

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The migration of the Hessian fly (*Mayetiola destructor* Say) larva on the leaf where it hatches to its feeding place between the leaf-sheath and the stem is one of the most critical periods in the life history of the insect, yet the literature on this point in the life economy is very meager. Packard (1883, p. 213) makes the following statement: "as soon as the footless larva or maggot hatches, it makes its way down the leaf to the base of the sheath." Osborn (1898), Thorne (1902), Felt (1902), Webster (1906 and 1915), Forbes (1910) and many others simply recapitulate the brief statement quoted from Packard.

Enock (1891, pp. 333-334) made some interesting observations on this point. He states that "the female fly, as a rule, lays her eggs with the head end pointing downwards towards the main stem, so that when the tiny larva emerges it is started from its infancy in the right direction on its journey downwards, and, guided by the longitudinal striae of the leaves, it reaches the stem, round which the leaf-sheath is closely wrapped, but not too close to prevent the larva forcing its way; until, after some four hours' steady travelling (during which time it has covered only the small distance of two or three inches), it reaches the base of the sheath." He also made some observations on the hatching of eggs that were laid " the *wrong* way, with the heads towards the *tip* of the leaf." In this case, " the larvae worked their way to the tip of the leaf, where some of them managed to cross the edge and get on to the back or under side, and commenced their tremendous journey of four or six inches ! some arriving at their destination at the next joint *below* the one they would have occupied had the female laid her eggs on the inside of the upright leaf."

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[1] Contribution from the Entomological Laboratory, Kansas State Agricultural College, No. 26. This paper embodies the results of some of the investigations undertaken by the authors in the prosecution of project No. 8, Kansas Agricultural Experiment Station.

Garman (1903, pp. 221-222) reports that " the eggs hatch in a week or less (three days in one instance observed), according to temperature, and begin their rather laborious journey to the leaf-sheath, during which they find even an egg or egg-shell an obstruction to be surmounted with difficulty. From the slowness of their progress the trip requires hours of time, and excepting as their minute size protects them, they are completely at the mercy of enemies. No doubt many of them are lost at this period of their lives." The same author states (p. 221) that when the eggs are laid on the lower surface of the leaf " the helpless young must have difficulty in finding their way between the leaf-sheath and the stem, with a good chance of perishing before this is accomplished, since it is their habit to follow closely the grooves in which they hatch down to the junction of blade with stem."

Gossard and Houser (1906, p. 4) report that the young larva " starts at once down the leaf, following the groove or crease in which it hatched, or an adjacent one, until it reaches the base; from this point it burrows between the leaf sheath and the stalk until it reaches the foot of the culm, ... While on this downward journey, which may occupy several hours, the young larva is easily deflected from its course by dirt particles or mechanical obstructions, and may lose its hold and fall to the ground, or may die, and in dried and shriveled condition remain for a time on the leaf." After performing some experiments to see if the larva could follow the creases of the blades up an incline, if it were necessary for the larvae to do this, in order to reach the base of the culm, they state (p. 5.) that "in no instance did a larva make more than a slight advance upward, and most of them died with their bodies extended crosswise of the creases, near the points where they had hatched." They add that the bearing of this experiment on the following statement quoted by Packard (1883, p. 212) is readily apprehended: "A reason given by some why the fly does not injure red wheat as much as white, is because the leaf of the red grows so long and slants down from the shoot, so when the egg hatches, the maggot works down the wrong way, falls to the ground, and so many fail to harm the wheat."

Headlee and Parker (1913, pp. 95-96) state that the larva "seems to have various means of getting down into the plant; some observations made by Mr. Kelly would indicate that in the presence of abundant dew it is washed down by the droplets of water. In other cases it undoubtedly crawls down, earthworm-like, following the groove until it reaches the place where the leaf-sheath winds tightly about the stem. Get down as it may, when once there it squeezes in between the leaf-sheath and the main stem and continues its way downward until it nearly reaches the point where the leaf takes its origin. Just above this point it stops and begins to feed."

METHODS OF STUDY

The experiments on which this paper is based were carried on in the breeding chambers of the air conditioning machine described by Dean and Nabours (1915). The temperature was maintained at approximately 70° and the humidity at about 70%. The wheat plants were grown in wide-mouth bottles containing Pfeffer's liquid plant food solution.[2] The roots of

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[2] Pfeffer's solution for wheat cultures is prepared as follows:

Calcium nitrate	4 grams
Potassium nitrate	1 gram
Magnesium sulphate	1 gram
Potassium dihydrogen phosphate	1 gram
Potassium chloride	0.5 gram
Ferric chloride	Trace
Distilled water	5 liters

the plants were kept in the liquid while the remainder of the plant was outside the bottle. The plants were held in place with a cotton stopper in the mouth of the bottle. This method proved very satisfactory because of the fact that the plants could be handled conveniently and the various stages of the fly could be studied with greater ease and exactness than when the plants were grown in soil.

OBSERVATIONS

Eggs.—The egg of the Hessian fly is very minute, being only about 0.5 mm. in length, cylindrical, obtusely rounded at the ends, glossy, translucent and pale yellowish red. This color deepens with the development so that just before hatching it is distinctly reddish in color. About the second day after deposition the posterior end of the egg becomes opaque, and shows no reddish content. This is very characteristic of the fertilized egg. The caudal extremity of the embryo is located in this end of the egg. Generally, the eggs are laid on the upper surface of the leaf, being glued into the longitudinal creases of the leaf-blade. Frequently the eggs are laid on the lower side of the blades of wheat plants, and occasionally on the stalk.

Hatching of Eggs.—The majority of eggs hatched in about 60 to 72 hours after deposition under the experimental conditions of the breeding chamber where the mean temperature was 70° F. and the mean relative humidity 70%. The exact method whereby the hatching occurs is not as yet ascertained. The egg-shell seems to split along its cephalo-dorsal aspect and the larva emerges quickly. Enock (1891, p. 333) records some observations on the hatching of the eggs. He found that the movements of the inclosed larvae could be distinctly seen on the third day and on the fourth day he was able to distinguish the muscular efforts of the larvae to burst open the shell, which they succeeded in doing after three or four hours work.

Orientation of the Larva.—Immediately after emerging from the shell, often before the body is more than one-half out of the egg-shell, the larva begins to turn sidewise, describing an arc and finally orients itself in the direction exactly opposite to that in which it had been within the egg (Fig. 1). This orientation behavior was first noticed when larvae, hatching from the eggs laid by a female held in an inverted position on the leaf during oviposition, instead of moving down toward the base of the leaf as the larvae were ordinarily known to do, moved up toward the tip of the leaf. In order to see if this seemingly abnormal behavior was merely accidental or really of regular occurrence, the following experiment was performed:

A young wheat plant was held in an inverted position and a female was allowed to oviposit on it. After the eggs were laid, the plant was turned right side up and kept under observation for the hatching of the eggs. Emergence occurred on the third day and the larvae turned away from the base of the leaf and moved up toward the tip of the leaf. This simple experiment was repeated a number of times and the result was always the same. Then the test was made with a number of modifications. In the first place, the influence of the orientation of the egg itself on the subsequent orientation of the larva was to be tested. In order to do this, it was necessary to have the eggs laid in as wide a variety of ways as possible, keeping in mind the possibility of such occurrence out in nature. Barring the minor modifications, there are three distinct ways in which eggs may be laid: (1) The eggs may be laid with their anterior end pointing toward the tip of the leaf. This is what happens in normal situations when the female stands on the leaf with her head toward the tip of the latter. Since this mode of oviposition by Hessian fly is the most general out in nature, and since this is the most natural way of ovipositing under ordinary circumstances, it will be designated in this paper as normal. (2) The eggs may be laid with their anterior end toward the base of the leaf. This is the situation exactly opposite to that of the first, and, undoubtedly, is of rare occurrence in nature. Only under forced conditions, and then with difficulty, will the female attempt to lay eggs while in an inverted position. Many such

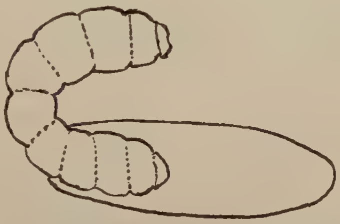

FIG. 1.—Hessian fly larva hatching from egg and turning toward posterior end.

attempts fail to bring about actual oviposition. The artificial method whereby the inverted eggs may be secured has been already described. The same result may be realized when the leaf is long and bends over, and the female alights beyond the bend with her head towards its base The base in this situation will be higher than the tip of the leaf. This mode of oviposition and the orientation of the egg will be here designated as inverted. (3) The eggs may be laid transversely or at varying angles with the long axis of the leaf. It is only necessary to mention that the three conditions described above are capable of modifications and also that they can be realized on the lower as well as on the upper surface of the leaf.

A series of experiments with eggs laid according to the methods stated above were performed, in connection with which more than three hundred larvae were studied and their behavior recorded. In no instance was the orientation of the larvae, soon after hatching, not in accordance with the expectation. Every one of the three hundred and more larvae turned towards the caudal end of the egg regardless of the manner of oviposition, position on the leaf, and in cases of inverted oviposition, regardless of the fact that this orientation leads the larvae away from the only possible feeding place, namely, the base of the leaf-sheath.

Migration of Larva on the Leaf.—The direction of movement, as has been stated, is predetermined by the orientation of the egg itself, and is not in any way influenced by the condition of the leaf upon which it is laid. After the initial orientation, the larva usually starts without delay on the journey down the leaf, following the first or second grooves adjacent to the one in which the egg was located. The movement is subject to variation in regard to the rate of progress, although generally it is a slow process. The larva may move continuously or it may rest now and then. When it reaches the base of the leaf or the ligule, it crawls up the latter, squeezes in between the leaf-sheath and the main stem, and continues its way downward to a point just above the joint or origin of the culm. In the case of inverted oviposition, the larva, on hatching, turns toward the tip of the leaf and this is the direction of its progress. It works its way slowly up the leaf, against the force of gravity, and constantly subjecting itself to danger of various sorts. When it reaches the tip of the leaf, it stops and apparently surveys the ground for a while, then getting by chance into another groove, it starts downward. Once on this course it works its way down in the same manner as the larva which came from an egg deposited in the normal manner. The behavior of the larvae hatched on the lower surface of the leaf is essentially similar to that of those on the upper surface. There was a tendency among the larvae from eggs laid in an inverted position on the lower surface to get over to the upper surface after they have gone up the leaf for some distance.

Rate of Migration.—Individual differences influence the rate of migration more than physical factors, such as the degree of inclination of the leaf, temperature, humidity, mechanical obstructions, and the like, although these factors always enter into the problem and need to be taken into consideration. The larvae which came from eggs laid in succession by the same female on the same leaf and in juxtaposition may not be able to move at the same speed. As a matter of fact, none of the larvae under observation moved according to any set of arbitrary standards. Tables I and II show the rates of migration of larvae when the eggs are deposited normally and when they are deposited in an inverted position.

TABLE I

RATE OF MIGRATION OF LARVAE HATCHED FROM EGGS LAID IN NORMAL MANNER

		Average time required to move 1 mm.	Average distance traveled
Total No. of larvae	205	4 min. 36.4 sec.	51.5 mm.
No. of larvae that got down into sheath	157	4 min. 1.6 sec.	53.3 mm.
No. of larvae died on leaf	48	6 min. 30.6 sec.	45.5 mm.

TABLE II

RATE OF MIGRATION OF LARVAE HATCHED FROM EGGS LAID IN INVERTED POSITION

		Average time required to move 1 mm.	Average distance traveled
Total No. of larvae	119	3 min. 38.7 sec.	99.3 mm.
No. of larvae that got down into sheath	51	2 min. 11.2 sec.	144.9 mm.
No. of larvae that died on leaf	68	4 min. 44.3 sec.	65.1 mm.

It is interesting to note that larvae hatched from eggs laid in inverted position, not only traveled longer distances on an average but traveled at greater rates than those that hatched from eggs laid in normal position. Table III is a comparison of the rate of migration up the leaf with the rate of migration down the leaf when the eggs are laid in an inverted position.

TABLE III

Comparison of Upward Migration with Downward Migration. Eggs Laid in an Inverted Position

		Average time required to move 1 mm.	Average distance traveled
Upward Journey—			
Total No. of larvae	30	3 min. 43 sec.	50.1 mm.
No. of larvae that got down into sheath	18	4 min. 29.2 sec.	38.0 mm.
No. of larvae that died on leaf	12	2 min. 35.3 sec.	70.2 mm.
Downward Journey—			
Total No. of larvae	12	3 min. 55.8 sec.	88.1 mm.
No. of larvae that got down into sheath	11	4 min. 10.5 sec.	89.5 mm.
No. of larvae that died on leaf	1	1 min. 38.0 sec.	73.0 mm.

Thus, as the table indicates, there seems to be no marked difference in the rate of progress during the journey in either direction, that is, the larvae, on an average, move with equal facility on either an ascending or descending incline.

Table IV is appended in order to give a little more accurate notion of the migratory rate, since these larvae were under closer observation.

TABLE IV

Rate of Migration of Twelve Selected Larvae Hatched from Eggs Laid in an Inverted Position

Larva No.	Upward Journey		Downward Journey		Entire Journey	
	Average time required to move 1 mm.	Distance traveled	Average time required to move 1 mm.	Distance traveled	Average time required to move 1 mm.	Distance traveled
	sec.	mm.	sec.	mm.	sec.	mm.
33-3	203	13	561	141	537	154
64-1	323	39	56	95	133	134
64-2	389	37	757	95	654	132
65-5	257	56	136	101	171	157
71-1	88	41	296	85	228	126
76-2	128	56	216	83	181	139

TABLE IV—*Continued*

	sec.	mm.	sec.	mm.	sec.	mm.
162-1	218	33	68	75	97	108
162-2	218	33	112	75	144	108
162-3	225	32	195	75	201	107
163-2	263	41	157	80	203	121
163-3	83	43	202	80	161	123
Average for 11 larva that reached the sheath	217.7	38.5	247.8	89.5	246.3	131.9
Larva that died on leaf	291	37	98	73	164	110
Average for 12 selected larvae	223.8	38.4	235.3	88.1	231.1	130.1

It may be of interest to note that there seems to be, as the preceding tables indicate, no correlation between the rate of migration and the distance traveled by the larvae resulting from two types of oviposition or between those larvae which died on the leaf and those that successfully reached the base of the plant. The maximum and minimum rates of migration when eggs are laid normally and when they are deposited in an inverted position are shown in Tables V and VI. Part 1 of each table gives the maximum and minimum average rates of migration with the distance traveled, while part 2 shows the maximum and minimum distance traveled.

TABLE V

MAXIMUM AND MINIMUM RATES OF MIGRATION OF LARVAE WHEN EGGS ARE LAID IN NORMAL MANNER

PART 1.—Maximum and minimum average rates of migration and distances traveled at these rates:

	Larva No.	Average time required to move 1 mm.	Distance traveled
Larvae that got down into sheath	231-1 Max.	27 sec.	131 mm.
	276-1 Min.	1800 sec.	2 mm.
Larvae that died on leaf	241-1 Max.	94 sec.	38 mm.
	277-4 Min.	4500 sec.	8 mm.

PART 2.—Maximum and minimum distances and rates of migration used to travel these distances:

	Larva No.	Average time required to move 1 mm.	Distance traveled
Larvae that got down into sheath	270-1 Max.	533 sec	162 mm.
	276-1 Min.	1800 sec.	2 mm.
Larvae that died on leaf	265-3 Max.	43 sec	84 mm.
	250-2 Min.	900 sec.	4 mm.

TABLE VI

Maximum and Minimum Rates of Migration of Larvae Hatched from Eggs Laid in Inverted Position

	Entire Journey		Upward Journey		Downward Journey	
	Average time required to move 1 mm.	Distance traveled	Average time required to move 1 mm.	Distance traveled	Average time required to move 1 mm.	Distance traveled
Part 1.—Maximum and minimum average rates of migration and distance traveled at these rates.						
Larvae that got down into sheath—						
No. 208-1 Max.....	24 sec.	294 mm.	?	139 mm.	?	155 mm.
No. 64-2 Min.....	654 sec.	132 mm.	389 sec.	37 mm.	757 sec.	95 mm.
Larvae that died on leaf—						
No. 221-1 Max.....	41 sec.	131 mm.	?	44 mm.	?	87 mm.
No. 226-1 Min.....	2769 sec.	26 mm.	?	26 mm.	0	0
Part 2.—Maximum and minimum distances and average rates of migration used to travel these distances:						
Larvae that got down into sheath—						
No. 208-1 Max.....	24 sec.	294 mm.	?	139 mm.	?	155 mm.
No. 70-1 Min.....	72 sec.	100 mm.	?	20 mm.	?	80 mm.
Larvae that died on leaf—						
No. 217-3 Max.....	46 sec.	158 mm.	?	98 mm.	?	60 mm.
No. 236-1 Min.....	300 sec.	12 mm.	300 sec.	12 mm.	0	0

According to Table IV, which records the behavior of 12 selected individuals which came from eggs laid in inverted position, there is absolutely no correlation of any sort between either the maximum or minimum speed and distance or maximum or minimum distance and speed. But Tables V and VI indicate that there seems to exist, so far as these particular individuals are concerned (although the same conditions apparently hold true in a number of other cases) certain correlations between the two items under consideration. The larvae which moved fastest traveled longer distances than those that moved slowest, and the larvae that traveled the longest distances moved faster than those that traveled the shortest distances. The rate of migration either on the upward or downward course, or on the upper or the lower surface of the leaf does not seem to be affected to any marked extent by the degree of inclination of the leaf. The leaf may have an inclination of anywhere between zero and 90 degrees, but the larvae seem to be able to move with equal facility in either direction. Acceleration or retardation, if any, due to the inclination of the leaf, usually is not appreciable; and even if it were of appreciable magnitude, it is better interpreted in terms of individual differences rather than due directly to any difference in the inclination of the leaf.

Variations in the Rate of Migration.—Every larva has a more or less different average speed from any other larva. Each larva has different speeds at different stages of migration. This variation in rate of migration in individual larvae can be seen in figures 2 and 3.

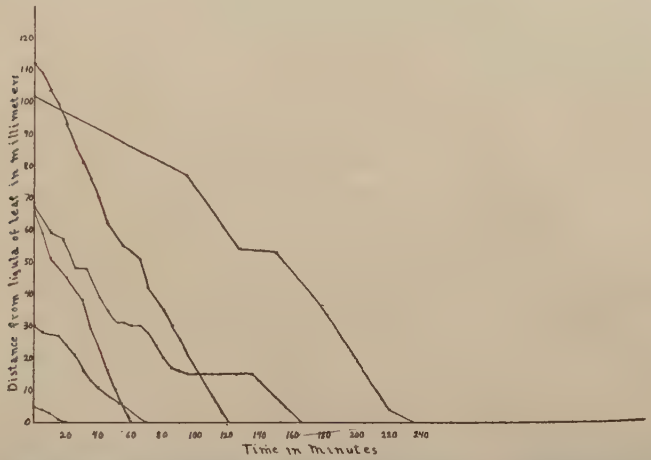

FIG. 2.—Chart showing the distance traveled and the rate of migration of six larvae hatching from eggs laid in the normal position. The dots indicate the location of the larvae at the time of observation.

As is shown in the figures, there seems to exist no regularity in the rate of progress in individual larvae. They may move faster at the beginning or toward the end of migration, or they may move fastest at the middle of the journey. Again, they may move for some time and then rest for an interval of from five or ten minutes to twelve hours or more.

Behavior of the Larvae on Migration.—The exact manner of the locomotion of the larva is hard to observe because of the minute size and the opaqueness of the wheat leaf. The larva seems to move in somewhat the same fashion as other footless insect larvae. The muscle tension coupled with the moist integument bearing intersegmented grooves and the rather rough, hairy condition of the creases of the leaf seem to operate in assisting the propulsion of the body of the larva. The process of orientation following hatching usually places the larva in a groove within the radius of the length of the body, which may be the first or second groove from the one in which the egg was laid. Once in a groove, the larva follows it down or up, as the case may be, until it reaches the end of the chosen path. In the case of normal deposition, this is the base of the blade where the short erect ligule which surrounds the stem arises. The ligule is a barrier which every larva must overcome, either by crawling over, as the majority of the larvae seem to do, or by avoiding it entirely by finding elsewhere a point of entry beneath the leaf-sheath. The larva, under favorable conditions, such as a clean, smooth ligule which is loosely wound around the stem, gets between the sheath and the stalk in a comparative short time. When the conditions are adverse, such as dirty, hairy, tight-fitting ligule and dry weather, the larva finds it extremely difficult to surmount the barrier and, in many cases, death overtakes it at this point, the usual mortality at this situation under experimental conditions being about 25%. The locomotion of the larva after it gets below the ligule has not been studied. When the larva, directed by the initial process of orientation, moves upward and reaches the tip of the

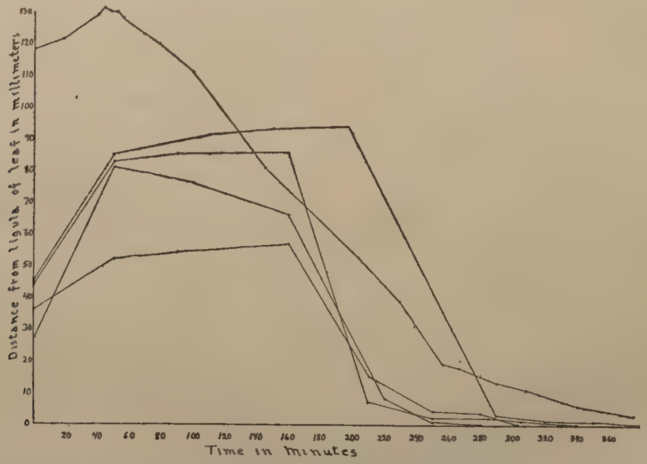

FIG. 3.—Chart showing the distance traveled and the rate of migration of five larvae hatching from eggs laid in an inverted position. The dots indicate the location of the larvae at the time of observation.

leaf where the grooves converge into a point at the extremity of the blade, it is then thrown upon its own resources in finding its way. It naturally performs random movements and in so doing it is likely to place itself now in inverted position in one of the grooves. This opens a way for the larva to escape the distracting maze of the tip of a leaf, and, after adjusting itself to the groove, it starts back down the long way it has so laboriously climbed up.

Variations in Behavior.—Although the larva is not known to refuse to turn round away from the direction of the anterior end of the egg, it may show individual differences or deviations from the ordinary course of behavior during migration on the leaf. Occasionally, a larva is found to cross the leaf-blade from one surface to another. This may happen at any point on the leaf but it usually takes place at or near the tip where the larva is forced to find a new way by random movements. When a larva meets an obstacle, e.g., a dirt particle, it usually seeks to avoid it by moving to an adjacent groove. Sometimes it may overcome the difficulty by actually crawling over the obstacle, or it may be forced to carry the impediment on its back, if the object is light enough to be lifted or pushed along. Small drops of water may wash the larva down away from the plant. A very small amount of water is found to be sufficient to trap the larva which loses it hold, and in case of a droplet, the maggot is not able to overcome the surface tension and free itself from watery imprisonment. It is not known whether the larva is capable of feeding on the leaf while migrating, although it seems to be the general feeling among the entomologists that it does not feed during this time. Enock (1891, 9, 334), however, states, that " the larva increases in width even before it disappears out of sight, leading one to suppose that it imbibes moisture as it journeys down the furrows of the leaf." Several cases of reversal of the direction of migration without apparent causes were noticed. In one case the larva, hatching from an egg laid on the lower side of the leaf, passed down to the stalk near the point where the latter passed into the culture solution. The larva turned around and started upward on the stalk which was standing vertically. After moving about 20 mm. the larva again reversed its direction of progress and started downward. In other cases, larvae were found to climb up the central stalk instead of crawling down into the culm. It is interesting to note that the larva seems to be unable to distinguish the right direction from the wrong when deflected from the former; e.g., larva 270-3, while moving down, was overtaken by larva 270-4, which forced it into the adjacent groove. The larva 270-3 was inverted completely by this treatment and when it started on its way was moving toward the tip of the leaf. This one died after moving 30 mm.

Mortality of Larvae on Migration.—The larvae, during their migration on the leaf, are in the critical period of their life and it is probable that many of them die. That such is the case is shown in Table VII, which gives the percentage of mortality of larvae from both normal and inverted eggs. Table VIII gives the details of the 68 larvae which hatched from the eggs laid in inverted position and which died on the leaf during migration. It is interesting to note that 53% of these larvae failed to reach the tip of the leaf. It is well to note, however, that these larvae had traveled the average distance of 56.6 mm. before they died.

TABLE VII

MORTALITY OF MIGRATING LARVAE

	Total No.	Larvae that got down into sheath	Larvae that died on leaf	Mortality, %
Larvae from eggs laid normal........	205	157	48	23.4
Larvae from eggs laid inverted.......	119	51	68	57.1
Total........................	324	208	116	32.7

TABLE VIII

ANALYSIS OF THE MORTALITY OF 68 LARVAE THAT HATCHED FROM EGGS LAID IN AN INVERTED POSITION

	Total No.	No. of larvae died on upward migration	No. of larvae died on tip of leaf	No. of larvae died on downward migration
Larvae from inverted eggs that died on leaf	68	36	8	24
Percentage.....................	100	53.0	11.7	35.3

Influence of Moisture.—The larvae seem to prefer moist air. Enock (1891, p. 335) found that "the progress of the young larvae was very much accelerated when the leaf was moistened, and many died on a hot, dry day." In a condition where the relative humidity of the air is 50%, the larva, if it ever hatches, has great difficulty in making its way down the leaf. In every case under this humidity the larvae failed to move but short distances and invariably died. Too much water, e.g., rain, will also be detrimental for then the larvae are likely to be washed away from the plant. Excessive dew may produce the same result.

Influence of Light and Darkness.—Not enough work has been done to justify any statement concerning the behavior of larvae under various conditions of light, but judging from the result obtained in an artificial cave where the light is very weak, the general behavior of the larvae seemed not at all modified from that in the bright light.

DISCUSSION AND CONCLUSIONS

The most interesting thing that was found so far as this study has progressed concerning the behavior of the larva, is the fact of orientation immediately following hatching. Regularity of its occurrence is significant. Possible advantages to be derived from this arrangement are not difficult to see. Since the eggs are laid normally with their anterior end pointing away from the base of the leaf, and since the larvae emerge from that end of the egg, the larvae must, under ordinary circumstances, turn round before they could possibly get down into the leaf-sheath, a process absolutely necessary for the life of the larvae. The orientation is therefore a distinct advantage to the larvae for it helps the latter to find their way quickly and properly. Furthermore, by being set in the right direction, the larvae are so directed as to minimize the period of exposure to the adverse conditions, for it is obvious that the sooner the larvae get down into the leaf-sheath, the safer they will be from the possible dangers, such as mechanical injury, attack from parasites and predaceous enemies, desiccation, etc. It is beyond the scope of this paper to discuss the force that is responsible for this phenomenon of orientation. Whatever the nature of this directing force may be, the fact of orientation certainly is an adaptation, a process distinctly advantageous in the life economy of the insect. As to the nature of the stimulus or stimuli in response to which the larvae manifest the migratory behavior, experimental data are lacking, but from the nature of the case, this phenomenon of migration might be interpreted as the result of positive thigmotropism and also possibly of positive geotropism. It is interesting to note that Enock (1891) found that the larvae moved towards the tip of the leaf when the eggs were deposited in an inverted position but he failed to notice the orientation of the larvae on hatching. Gossard and Houser (1906, pp. 4-5) seemed to have had difficulty in making the larvae ascend a slope of about 45 degrees. In the present work, however, it was found that the larvae are not only able to ascend an inclined leaf (to the height of 139 mm., in one case) standing almost perpendicularly, but they do so regularly if the eggs are laid in an inverted position.

The reason quoted by Packard (1883, p. 212) why the red wheat is less injured by the fly than the white wheat needs revision, because the sloping leaf has nothing directly to do with the larvae working down " the wrong way." Whether the larvae are assisted by dew in their migration down the leaf blade, as suggested by Headlee and Parker (1913, pp. 95-96), needs, in the writer's opinion, closer scrutiny for the data on hand seem to indicate that the larvae find great difficulty in overcoming the surface tension of drops of water and, furthermore, dewdrops do not always roll to the base of the leaf-blade and stop there until the larvae are safely discharged.

SUMMARY

1. The direction of the migration of the larva in its initial stage is predetermined by the orientation of the eggs. The larvae on hatching always turn from the anterior toward the posterior end of the eggs.

2. The degree of inclination of the leaf has nothing to do with the direction of the larval migration.

3. The larvae are capable of locomotion on either an ascending or descending incline of anywhere between zero and 90 degrees.

4. When the eggs are laid with their anterior ends toward the base of the leaf, the larvae, on hatching, crawl up the leaf

until they reach the tip, then turn and move downward. The larvae may die while on this ascending migration but apparently never try to change the direction of progress.

5. The rate of migration is extremely variable and seems to be influenced by individual differences rather than physical factors. The average time required by 205 larva hatching from eggs laid normally to move one millimeter was about four and one-half minutes, with extremes of one-half minute and seventy-five minutes. The average time required by 119 larvae hatching from eggs deposited in an inverted position to move one millimeter was about three and one-half minutes, with extremes of two-fifths of a minute and forty-six minutes.

6. The mortality of migrating larvae is greatest when the eggs are laid in an inverted position. Twenty-three per cent of the larvae hatching from eggs laid normally died on migration, while fifty-seven per cent of the larvae hatching from eggs deposited in an inverted position perished.

7. When the eggs are deposited normally, the per cent of mortality increases with the distance of the egg from the ligule. When the eggs are laid in an inverted position, the mortality increases with the distance of the egg from the tip of the leaf.

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REACTIONS OF OPALINA RANARUM

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1. INTRODUCTION

Although the anatomy and reproduction of Opalina ranarum have been carefully studied, the reactions of this mouthless entozoic infusorian have not been so thoroughly investigated. Probably the most comprehensive recent work is that of Metcalf ('09) who gives a splendid chronological review of the literature. The first account, however, which deals with reactions, is that of Kühne ('59) who describes the effect of a strong induction current on Opalina. Several years later, Nussbaum ('86) briefly described the structure and the method of swimming in the introduction to his theme on reproduction. In 1888, Entz worked on light reactions and concluded that Opalina was negative to light. A year later, Verworn ('89) obtained results on the effect of light which were exactly opposite to those of Entz. Verworn treats also of reactions to heat stimuli.

Experiments in galvanotropism were performed by Birnkoff ('99), Pütter ('00), Kölsch ('02), Wallengren ('03), and Hartog ('06). Dale ('01) gives the most detailed account yet published of chemotaxis and describes very carefully the movement of cilia and their behavior to chemical and electrical stimuli. Veneziani ('04) experimented with culture media of varied chemical composition and showed the effect of each on Opalina. His work was continued by Pütter ('05) who discovered that a medium prepared from sodium chloride, sodium and potassium tartrate and distilled water was best. The work of Jennings ('06) concludes the list of publications on the behavior of Opalina.

Opalina is a large ovoid protozoan completely covered by a pellicle and therefore without mouth or anus.[1] It is strongly flattened dorsoventrally and somewhat asymmetrical at the more pointed anterior end of the "adult" animal, (Fig. 1). From the anterior end to the notch, in the middle of the right side, the surface of the body is concave, and below the notch, this side is markedly drawn in. The left side shows no such irregularity. Cilia are distributed abundantly over the entire pellicle; on the dorsal and ventral surfaces. They are arranged in diagonal rows across the body. Small Opalinas or those formed by recent divisions usually have the posterior end more pointed than the anterior.

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[1] Some of the earlier investigators (Künstler, '06, and Gineste, '06) claimed that a minute mouth was present on the ventral surface of the body, but their view has not been accepted by recent observers. The writer has made every effort to discover such an opening but without success. Specimens stained slightly with Delafield's haematoxylin and placed in a thin solution of gelatin afford excellent opportunity for observation but nothing could be discovered except little evanescent folds which frequently appear when the body is in the proper position.

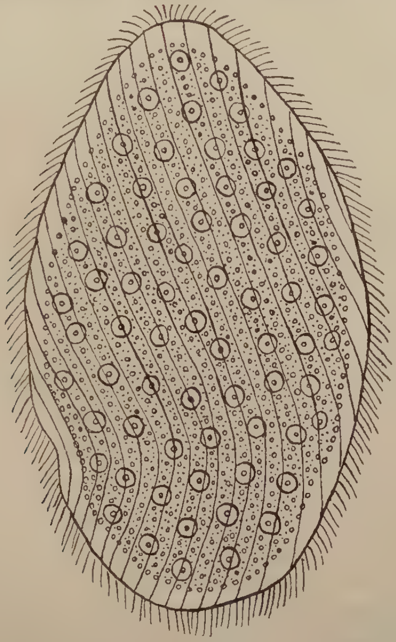

FIG. 1.—*Opalina ranarum.* Ventral view (after Dolflein)

The object of the present paper is to present a general account of the behavior of Opalina and to compare its reactions with those of free-living protozoans which are well known through the work of Jennings, Mast, and others.

The experiments discussed in this paper were performed in the Zoological Laboratories of the University of Wisconsin during the months of January, February, March and April, 1915. My thanks are due to Professor A. S. Pearse, under whose direction the work was done. Practically all material used was obtained from the rectum of leopard frogs, *Rana pipiens*, which were kept in a tank of running water in a vivarium. Although the room was heated, the temperature of the water ranged from 2° to 10°C.

Zeller ('76) observed that large Opalinas seemed to be absent from frogs in the month of January. This might be the case if frogs are allowed to remain in their natural habitats. During the present observations, however, Opalinas were apparently normal throughout the winter, though all frogs examined were not infected. Dobell ('07) pointed out that lack of food and increase in the number of bacteria in the rectum of the frog were causes of degeneracy in Opalina. In several instances, the writer noted that Opalinas were not found when there were no faeces or when the bacteria were few in number. The largest numbers were obtained when there was a considerable quantity of faeces and when the number of bacteria was comparatively large.

Material for observation was usually obtained from a frog by pithing or quickly chloroforming it. Pütter's saline medium, already mentioned, or a physiological salt solution made suitable culture media except when chemical stimuli were used. In the latter cases, it was found that by forcing water down the alimentary tract of the frog, a sufficient amount of liquid to serve as a medium for observations could be obtained without interfering with the normal activities of the Opalinas. When the medium was ready for use, enough was dropped on an ordinary slide to nearly cover one-half of it. If another liquid was introduced, it was carefully added with a dropper drawn to a fine point. Frequently the drop of chemical was placed next to the medium containing Opalinas, and then by the aid of a needle, was induced to flow across gradually. Experiments with colored liquids showed that diffusion took place quite slowly and that sometimes the introduced drop remained in only a small portion of the medium. A cover glass was usually not used.

OBSERVATIONS ON LOCOMOTION

Considering the environment of Opalina, it may be justly called a comparatively active creature, especially immediately after division. Other investigators have noted that the smaller individuals are extremely active and swim rapidly as if in a state of excitement. Unless stimulated, the mature Opalina moves very smoothly and bends its body gracefully as it wanders in and out among the debris. Finely ground India ink and gelatin were used successfully in observing the movements. Opalina was frequently found at rest either at the edge of a drop of culture medium or against a bit of the faeces. It keeps its cilia in active motion, however, at all times and apparently does not attach itself in the same way that Chilomonas, Didinium, and Paramoecium do.

The action system is essentially like that of many free swimming ciliates and flagellates. Opalina usually swims through the water in a spiral course, but quite often one is seen swimming without revolving on its long axis. Like many other ciliates, such as some Hypotricha and Colpidium, it often swims forward keeping one side against an object or in contact with the edge of a drop of liquid. In making its screw-like revolutions, Opalina turns over to the right. It was noted that Opalina does not make as many revolutions for a given distance as Paramoecium. Sometimes, it makes only half-revolutions at varying intervals, and then turns over toward the left for a time. There is another characteristic movement which does not seem to have been noted in other ciliates. Frequently, after making half a revolution, an Opalina will turn back the same distance, and repeat this movement several times in rapid succession.

The spiral course is much like that of Paramoecium as described by Jennings ('06). There are two factors which seem to influence this particular type of movement in Opalina—the forward movement of the animal, and the rotation on the long axis to the right. Cilia extending from the left to the concave edge on the right, beat directly backward and bring about the forward movement. The rotation on the long axis is due to the fact that the cilia on the surface of the body beat obliquely to the right and backwards. The revolving to the right is probably partly due to the asymmetrical form and partly to the cilia at the anterior end which beat obliquely forward. If all the cilia beat directly backward the animal moves forward without rotating. The cilia on the surface of the body beat in a rhythmic wave-like manner. Objects, caught in the cilia at the anterior end, were carried down the surface of the body in jerks. The cilia on a pair of conjugating Opalinas beat in harmony until the animals are ready to separate and then each set of cilia beats so as to part the pair.

AVOIDING REACTIONS

Opalina reacts to stimuli by using avoiding reactions similar to those of Paramoecium, Chilomonas (Jennings, '06) and Didinium (Mast, '09). It backs for a short distance without revolving on its long axis, and after turning to the right, swims forward at an angle to the original course. Sometimes the angle may be as much as 90.° An Opalina may make " tests " in several directions, moving forward or to the side, trying the conditions until they prove to be satisfactory. When reacting to some stimuli, Opalina swims in a circle without revolving and keeps the left side away from the center of the circle. Certain stimulating agents cause it to turn " somersaults " by bending up the anterior end and going over and over, but this type of reaction was not common.

In several instances it was possible to be very certain of the exact position of the body during rapid movements on account of a little blister or some other peculiarity. Individuals which came in contact with objects did not always back away but sometimes turned directly to the right. The locomotion of a conjugating pair is similar to that of single individuals.

REACTIONS TO MECHANICAL STIMULI

While swimming in a normal medium, Opalina frequently comes in contact with various objects and responds by the avoiding reaction already described. It may not retreat at all, however, but become fixed against a bit of faecal matter and remain in contact with it for some time; the behavior resembling Paramoecium against a bacterial zoögloea. If bits of filter paper are put into the medium, Opalina responds when it touches them with the avoiding reaction, or merely rests against them, beating its cilia as it does when standing against faecal debris. Occasionally, it moves along the edge, keeping the body close against the paper.

The ability to select food is not as evident in Opalina as in Didinium or Lacrymaria (Mast, '09, '11). Opalina does not readily discriminate between organic or inorganic matter for it will rest against a glass rod, a needle, or bit of filter paper, as readily as against faecal debris. Particles which might contain food are brought to the resting protozoan by the vigorous stroke of the cilia.

When the anterior end of Opalina is touched by a fine needle or a glass rod, the animal usually responds with the avoiding reaction. If the same stimulus is applied to the side of the body, there is usually no reaction, although there is occasionally a forward movement. Opalina will allow itself to be pushed along with a needle without attempting to move away.

REACTIONS TO CHEMICAL STIMULI

In studying the reactions of Opalina to chemical stimuli the fluid contents of the frog's rectum served as a medium in order to have conditions as normal as possible. This was usually alkaline, but sometimes slightly acid, and though such variations may have caused discrepancies they were probably neglible. Dale ('01) has carefully worked out the chemotaxis of Opalina in alkaline, acid, and neutral cultures. Opalina showed positive reactions to acids and negative to alkalies; but in an acid solution was negative to stronger acid and positive to alkali.

Although Opalina resembles Paramoecium in its responses to chemicals, it is usually slow in reacting to stimuli. It oftentimes swims quite a distance into a strong solution before reacting. The chemical, if injurious, proves fatal before the animal can make its escape. Usually, however, an Opalina will swim up to the border of a chemical solution and turn directly to the right. Like Paramoecium, Opalina sometimes enters and swims directly across a drop of a solution without response until it comes in contact with the original liquid on the other side, where it gives the avoiding reactions. As Dale ('01) pointed out, Opalinas are occasionally seen in clusters which are probably due to the presence of carbonic acid. The writer noted that Opalinas were frequently grouped together when taken from the rectum. As Mast ('12) noted in the case of Peranema, there was no evidence of orientation with regard to the direction of diffusion of the stimulus. Chemicals sometimes caused Opalina to swim in circles without revolving on the long axis.

When Opalina is dropped into distilled water, it swims hurriedly about for a time. Tap water placed next to a drop of culture medium was avoided for a short time, such water is less dense than the usual medium. Dilute salt solution induces the avoiding reaction when Opalinas are transferred to it from the rectum of a frog.

If an iodin-green or methyl-green crystal is dropped into a culture medium of Opalinas, they will respond by the avoiding reactions (Fig. 2). In some instances, they collected around the crystals but, as they are very susceptible to these chemicals, in a short time even comparatively dilute solutions caused death. Peranema (Mast, '12) is apparently much more resistant to the effect of iodin-green, methyl-green, and methyl-blue. Opalina avoids methyl-orange and a .4% solution of methylene blue (Fig. 2). If, by chance, it has ventured into these chemicals, it will turn to the right without revolving or backing, and find its way out. It was noted that some Opalinas which swam

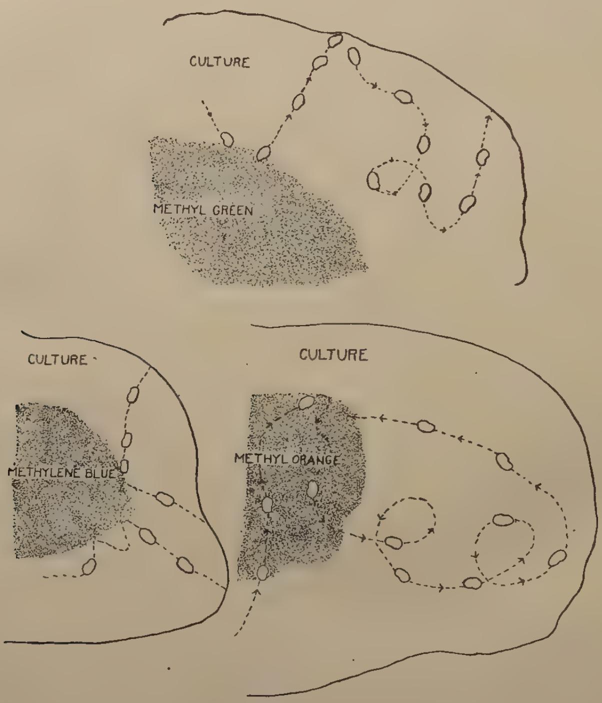

FIG. 2.—Showing reactions to chemicals

around in the chemical for some time would respond when encountering the culture medium.

Opalinas collected about acids introduced into the alkaline culture medium. Opalina is more susceptible to hydrochloric than to acetic acid. In one case, it was noted that Opalina lived in .01% solution of acetic acid for fifteen minutes before it proved fatal. Opalina reacts positively to nitric, sulphuric and formic acids. Even when acids were quite concentrated, it does not give avoiding reactions. The concentrations used varied from N–500 to N–10,000.

Opalina avoids neutral salts and those exhibiting basic properties. If a .2% solution of sodium chloride is added to the medium, Opalina, like Spirostomum (Jennings, '00) will avoid it by turning to the right and swimming off in a new direction. Opalina also responds by the avoiding reaction to a .005% solution of potassium hydroxide. It also is negative in its reactions to .02% to .002% solutions of each of the following salts: ammonium chloride, calcium chloride, potassium chloride, and a similar per cent solution of sodium hydroxide. In one case in which calcium chloride was used the strong repellent action was particularly noticeable; a large number of individuals, near the salt, moved away and crowded together at the opposite end of the slide.

TEMPERATURE

Unlike Paramoecium and Oxytricha, Opalina does not give the avoiding reactions to change in temperature. As Verworn ('89) observed, it swims indifferently from a warmer to a colder area and vice versa. If a quantity of culture medium, heated to about 40° C., is put on one end of the slide, Opalinas coming in contact with the warmer liquid swim actively about. When they approach the center of the heated area, motion ceases entirely, the cilia continue to vibrate rapidly for a few minutes, and then stop beating; the entire animal soon disintegrates. That Opalina is not very resistant to heat is shown by the fact that if it is allowed to remain in a temperature above 22° C., it dies in a short time. If Opalina is dropped into a heated medium, it does not respond by the avoiding reaction as has been observed in Pleuronema (Jennings, '06). Opalina shows a very great resistance to extremely low temperatures. It does not react to water at 2° C.

Temperature reactions were also studied by siphoning water of various temperatures through an exceedingly fine capillary U-shaped tube. With this apparatus a more uniform and definite temperature was obtained. The tube which rested on the slide was observed under a microscope. Opalina swims indifferently up to the cold or warm tube, rests along the surface or may move along in close contact with it.

REACTIONS TO LIGHT

Light induces no change in the movements of Opalina as is also true of Paramoecium and other colorless ciliates. Neither an increase in intensity nor a decrease causes a response. Contrary to what Entz ('88) observed, Opalina may be suddenly exposed to very bright sunlight and then quickly shaded without causing it to react. There was no evidence that it oriented in horizontal rays of light. In one instance, where a number were oriented in the direction of the source of light, there was no response when the slide was turned 180°. Polarized light or red light have no effect on movement.

In some of the experiments with light a Nernst lamp of about 650 candle power was used in a dark room. By moving the light to various distances, varying from 12-178 inches from the Opalinas, different intensities were obtained but no reaction was noted.

SUMMARY

1. Opalina usually swims in a spiral, though it frequently travels long distances without rotation, or moves along the surface of some object without turning over. When feeding it remains in contact with the debris and keeps the cilia vibrating rapidly.

2. The spiral course is due to the forward movement of the organism and the rotation on its long axis. Opalina often makes half a revolution and then turns back the same distance.

3. Opalina reacts to stimuli by moving backward a short distance without rotating and then turning to the right at an angle to the original course. If it is stimulated, it "tries" many different directions until one is found which proves satisfactory. When stimulated Opalina often swims in a circle, without revolving, keeping the left side turned away from the center.

4. Mechanical stimuli sometimes induce the avoiding reaction. Opalina frequently swims indifferently up to glass, needle, filter paper and other objects, remaining against them as if in contact with food. Opalina responds by retreating when the anterior end is touched with a fine rod but does not react when the side of the body is stimulated.

5. Opalina lives in both acid and alkaline media. When in an alkaline medium it reacts positively to acids and negatively when encountering neutral and basic salts. It may cease to react to a chemical after repeated stimulation and remain in the chemical. Solutions of different strengths cause the avoiding reaction when Opalina swims from one to the other. Opalina does not avoid strong acids.

6. Opalina does not react to heat or cold. It is much more resistant to cold than to heat. It may live at temperatures of from 2° C. to 22° C.

7. Light apparently has no effect on the orientation or movement of Opalina.

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SIMILAR BEHAVIOR IN COW AND MAN WITH A NOTE ON EMOTION

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The two incidents herein described present features of such similarity that they seem worthy of record among investigations bearing on comparative problems and especially among statements concerning instinctive (?) tendencies.

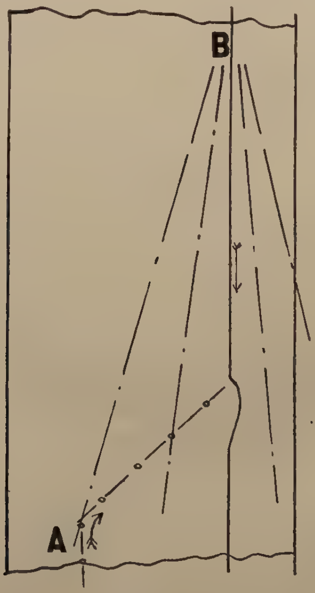

Fig. 1

Fig. 1 gives the essential features in the setting of the first incident. The Jersey cow was walking along the side of the road toward us, near the position marked A, when the light of the automobile at B, first disclosed her presence. As the car approached her, going in a straight line as indicated, she turned in an easy curve, not abruptly, and walked in the direction indicated. The distance across the road was relatively short, so that by the time the car reached her, the driver was forced to swerve the car sharply to our left to avoid hitting her head with the front fender of the car. As the front end of the car passed, the cow jerked her head sharply to the left and thus avoided collision with the rear end.

The incident occurred about seven o'clock in the evening. It was sufficiently dark so that objects to the human eye, when dark adapted, gave only indistinct outlines. In the lighted roadway in front of the car objects such as sticks, stones, and uneven places in the road-bed could be seen distinctly. At least four possibilities are open. The behavior of the cow may indicate some form of heliotropism, or the difference in distinctness of pathways may have operated to change the animal's behavior. A third hypothesis might combine the two factors suggested. We may also designate this behavior as habitual.

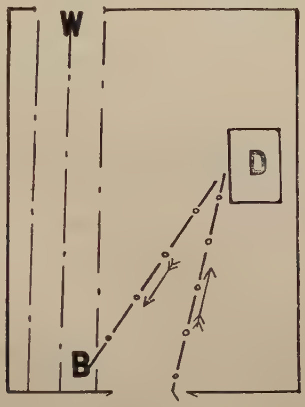

FIG. 2

Fig. 2 gives the surroundings of the second incident. My office is next door to the room outlined in the diagram. I was working by electric light one evening at my own desk and had occasion about eight o'clock to place some papers on the desk of this adjoining room. I entered the room, laid the papers on the desk, and returned to my own office. On my return, I found I had failed to replace all of the papers. Picking up those remaining, I retraced my steps. I placed the second set of papers with the first and started to return. On reaching the location indicated, B, my head jerked back and I turned abruptly to my left. I was not approaching the door as can be seen from the diagram.

For the first time, I now seemed aware of the setting of the situation in which I had just reacted as described. The moon's rays were shining through the window W, and lighted up an area of the wall and a few inches of the floor back of the spot marked B. The lighted area was about three feet wide and extended up two feet on the dark gray wall. In the corner of this illuminated area was a small, round gas stove and a few strands of insulated wire loosely coiled. The moon's rays did not reach the doorway by which I was attempting to pass out. The point reached, B, is approximately five feet from that one usually passed over in going out of the room by daylight.

Up to the point of the second change in pathway in order to avoid the wall and to go out by the door, the reactions of the cow and of myself are similar. Objectively the incidents may be described in identical terms and no one can seriously urge that consciousness took any prominent part in either subject's behavior. In the two cases, we have positive reactions whose settings are strikingly similar; and in the cow's head jerking to the left and in my own head jerking back, we can see the typical withdrawal reaction. Anecdotes are plentiful of horses and cows refusing to be driven from the lighted areas around burning barns, etc., but I can at present recall no case of so direct a human response to lighted areas, uncomplicated by implications of inner purpose.

The explanations suggested above for the cow's behavior appear accurate and complete here also.

After making the withdrawal reaction of the second trip, my consciousness of the situation included a distinct and clear revival experience accompanied by feelings of astonishment and excitement. My behavior now differed materially from the first form. I stopped, looked at the lighted area, turned around toward the window, and left the room slowly. No one who has made the two trips or had seen them made could avoid the conclusion that a distinct change in behavior had taken place. I now *knew* definitely that I had taken the wrong path on the *first* return trip also. (I fear the behaviorist will not read much further.) But the shift from the pathway toward the lighted area to that through the doorway the first time must have taken place quite smoothly for I can find no memorial evidence and no hints indicating perseverative tendencies in the recollections of the interval between the two trips. Nevertheless, after the second trip, I remembered the reaction of the first. Theoretically, the first reaction and the whole first trip must have persisted and modified the behavior on the second journey. For example, I could recall a slight, but noticeable increase in the speed of my movements as I placed the forgotten papers with the others,—placing these papers on my colleague's desk would close my work at the office for the evening. We may then postulate two new factors in the conditions of the second trip; on the evidence of recall, there was the perseverative influence of the first reaction; and there is distinct introspective evidence of a slight annoyance over the necessity of repeating the process.

Looking back over the few moments involved, I can find no form of evidence for believing that I was aware of going toward the lighted area. The instinctive or habitual behavior and the conscious processes seem ideally teased apart in the incident. The details of my thoughts were about the contents of the papers and my trip homeward; and I am unable to connect any portion of the mental process with the change in behavior that led away from the door on both return trips, and announced itself so vividly on the second. On the other hand, the mental processes connected with the behavior during the emotional excitement that followed the second reaction are clear. The kinaesthetic wave that localized itself in the muscles of the neck, shoulders, chest, and upper arms was distinctly noted at the time. Detailed thoughts about the lighted area, the relation of pathway to desk and door, astonishment at the sudden movements made, and a diffused intellectual excitement accompanied the later wavering behavior above described.

We cannot omit to recall in this connection, Professor Dewey's suggestions concerning a theory of emotions. Although the total equilibrium is not laid bare, nevertheless, the only ground for astonishment and excitement seems to rest in the sudden breaking of the steady progress toward the lighted area on the wall by the energetic jerk of the head backward. "What to do about it" is thrust forcibly into the foreground of consciousness. Briefly, we see that objectively the reactions of the cow and of the human are describable in the same terms. In the latter no preliminary conscious process is discovered to explain either the reaction to light or the withdrawal reaction. The conflict between the positive reaction to light and the avoidance reaction are the immediate precursors of a definite emotional state.

FREQUENCY AND RECENCY FACTORS IN MAZE LEARNING BY WHITE RATS

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Let us assume that the number of previous runs in any unit of the maze (frequency) determines the direction a rat running the maze in the process of learning will take at any bifurcation encountered, and that probability alone governs the early " choices " at such positions.[1] On these assumptions an interesting explanation of maze-learning by rats has been made. Let us start an imaginary rat in a ten-*cul-de-sac* maze and determine its course at each bifurcation by flipping a coin: " heads," it keeps its direction—forward or return, in whichever it happens at the time to be going; " tails," it enters the blind alley. On emergence from the blind alley, " heads " again takes it in the direction it had when the blind alley was encountered and " tails " means a return, the reverse of that direction.

The results of one such trial are here given to make more concrete the method. F in the lower line means movement toward the food box (forward) and R signifies a return, the reverse direction. An R *underscored* means that the return is complete and that the direction of movement is reversed, putting the animal again at the first bifurcation—at the first blind alley. The figures represent blind alleys entered.

h	t	h	t	h	t	t	t	h	t	h	h	h	t	h	t	t	h	t	h	h	h
F	2	F	3	F	4	R	3	R	2	R	*R*	F	2	F	3	R	R	1	*R*	F	F

h	t	t	h	t	h	h	h	t	t	t	h	t	t	h	h	h	h	t	h	t	h
F	4	R	R	2	R	*R*	F	2	R	1	*R*	1	*R*	F	F	F	F	5	F	6	F

t	t	t	t	h	h	h	h
7	R	6	F	F	F	F	F (to food box).

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[1] Throughout this discussion the word "choice" is used in the sense of going into one of two possible alleys open to the animal at any given bifurcation in the maze, not as implying any voluntary selection.

Figure I, a schematic maze with ten blind alleys, will make the results clear as recorded. The reader should keep the rule in mind and follow the rat through in detail. It will then be clear why a returning animal emerging from a blind alley gets F for a *t* and a second F for an immediately succeeding *h*, and *vice versa*.

Numbering and lettering the sections of the maze as shown in the figure, we may tabulate the choices of our hypothetical rat at the several bifurcations in a convenient manner for close inspection (Table I). The data of the first trial, already given on the previous page, are here tabulated as "trial 1." The other trials were made in the manner already described. The four trials are sufficient to illustrate the point in mind, and the method of analysis to be applied to results of actual rats learning the maze. In the table the letters Fd and Rt in the second column, under the caption "direction," show whether the animal was running forward or whether it was returning when the scores in the line in question were made. Thus the record starts with the animal passing *cul de sac* 1 and entering 2. That is, the first choice is B, the section of the correct path, the next is the second blind alley; then the forward direction is taken on emergence from 2, and 3 is entered; again the forward direction, and 4 is entered. From this point the animal makes a complete return, entering 3 and 2, but not 1 on the way; and so on. The summary of results of the individual trials and the general summary of the four trials show separately, for each lettered section of the maze, the total runs for each direction—Fd and Rt. In the case of the blind alley sections these two sets of totals, for forward and return runs, are combined, since the animal traversed those units in the same direction whether the blind alley was entered on a forward or on a return movement.

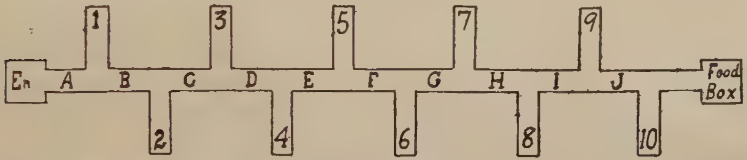

FIG. 1.—A schematic maze to show the lettering and numbering of the different sections. Numbers indicate blind alleys.

TABLE I

	Maze											Parts									
Direction	A	1	B	2	C	3	D	4	E	5	F	6	G	7	H	8	I	9	J	10	Food Box
Trial 1—Fd......			1	1	1	1	1	1													
Rt......	1		1	1	1	1	1														
Fd......			1	1	1	1															
Rt......	1	1	1		1																
Fd......			1		1		1	1													
Rt......	1		1	1	1		1														
Fd......			1	1																	
Rt......	1	1	1																		
Fd......		1																			
Rt......	1																				
Fd......			1		1		1		1	1	1	1	1	1							
Rt......												1	1								
Fd......													1		1		1		1	1	1
Totals...........	5	3	5 4	5	4 3	3	3 2	2	1	1	1	2	2 1	1	1	0	1	0	1	1	1
Trial 2—Fd......		1	1	1																	
Rt......	1		1																		
Fd......		1																			
Rt......	1																				
Fd......		1																			
Rt......	1																				
Fd......			1	1																	
Rt......	1		1																		
Fd......		1	1	1	1		1	1	1	1											
Rt......	1		1	1	1	1	1		1												
Fd......		1																			
Rt......	1																				
Fd......			1	1	1		1	1													
Rt......				1	1	1	1														
Fd......					1	1	1		1		1		1	1	1		1		1		1
Totals...........	6	5	4 3	6	3 2	3	3 2	2	2 1	1	1	0	1	1	1	0	1	0	1	0	1

TABLE I—*Continued*

	MAZE										PARTS										
Direction	A	1	B	2	C	3	D	4	E	5	F	6	G	7	H	8	I	9	J	10	Food Box
Trial 3—Fd.....		1	1		1		1	1													
Rt.....				1	1		1														
Fd.....					1	1	1	1	1	1											
Rt.....						1	1	1	1												
Fd.....							1		1	1											
Rt.....	1		1		1	1	1		1												
Fd.....		1	1	1																	
Rt.....	1	1	1																		
Fd.....		1	1		1	1															
Rt.....	1		1	1	1																
Fd.....		1	1		1		1	1	1	1	1		1	1							
Rt.....										1	1	1	1								
Fd.....											1	1									
Rt.....						1	1		1	1											
Fd.....							1		1		1	1									
Rt.....		1	1		1		1	1	1		1										
Fd.....			1		1		1	1	1		1		1		1		1		1	1	
Rt.....												1	1		1		1		1		
Fd.....													1		1		1	1			
Rt.....																1	1				
Fd.....																	1	1	1	1	
Rt.....																		1	1		
Fd.....																			1		1
Totals..........	3	6	5 4	3	5 4	5	6 5	6	5 4	5	4 3	4	3 2	1	2 1	1	3 2	3	3 2	2	1
Trial 4—Fd.....			1		1	1															
Rt.....	1	1	1		1																
Fd.....			1		1	1	1		1		1	1									
Rt.....						1	1		1		1										
Fd.....							1	1	1	1											
Rt.....		1	1		1		1	1	1												
Fd.....			1	1	1	1	1	1	1	1	1	1									
Rt.....						1	1		1		1										
Fd.....							1	1	1		1		1		1		1	1	1		1
Totals..........	1	2	3 2	1	3 2	5	4 3	4	4 3	2	3 2	2	1 0	0	1 0	0	1 0	1	1 0	0	1
Totals of 4 trials	15	16	17 13	15	15 11	16	16 12	14	12 8	9	9 5	8	7 3	3	4 0	1	6 2	4	6 2	2	4

The totals are very interesting and seem to throw some light on maze learning. As would be expected on laws of probability, the numbers at the entrance end of the maze are much larger than those at the food end, though the diminution in the size of the numbers as the food end of the maze is approached (the right side of the table) is not entirely regular. This general decrease in the numbers toward the food end of the maze is obviously due in the main to the fact, not usually pointed out in maze learning, that any animal entering the food box does not return. This is not due simply, if at all, to the *pleasure of eating*; it is due to the conditions of the experiment. An animal entering the food box is *prevented* from returning. There are consequently on our record no returns in the section of the maze leading from *cul de sac* 10 to the food box. Hence, moreover, only one-fourth of all runs reaching 10—whether the animal enters or goes beyond it—result in returns from this point. This is the expectation statistically and our results of the four "trials" of the hypothetical rat only approximate this expectation, —2 to 4. As we shall see, this is a point of much significance which seems to have been overlooked in studies on maze learning.

In these results, derived by the laws of chance, the totals for all forward movements in the lettered parts of the maze—the sections making up the true path—amount to 96. For ease of detection these numbers are in bold face in the totals column. The total entrances to blind alleys are 88; and there are in all 71 returns over the lettered sections of the maze. These numbers come close to probability expectations, as will be shown. A forward-direction approach to any blind alley gives a probability of 1/2 that the blind alley will be entered and 1/2 that the correct path will be kept. If the *cul de sac* is entered the animal will return to the true path, at which point the probability is again 1/2 that the forward direction will be taken and 1/2 that the return direction will be chosen. This makes a total probability of 3/4 (= 1/2 + 1/2 of 1/2) that the animal will keep the general forward orientation whether or not the blind alley is entered, and of 1/4 that it will be turned back at the blind alley (*i.e.*, 1/2 of the blind alley entrances will result in returns).[2] In general, of x approaches to any blind alley in the forward direction $x/2$ entrances to the blind alley in question will be made; $x/4$ returns will be made from this point; and $3x/4$ cases of keeping the general forward direction will occur. But on any return trip past the same blind alley these probabilities are reversed; there is now in x such cases a probability of $x/2$ that the blind alley will be entered, of $x/4$ that the forward direction in the maze will be resumed, and of $3x/4$ that the return direction will be maintained. Adding these fractions to those for corresponding directions above, we get a probability of x for entrance to the blind alley, of x for the forward direction, and of x for returns. That is, for any equal number of forward runs in the maze and returns to the place of starting—with the forward and backward intermediary movements that according to chance would result—the probability of entrances to blind alleys, of return directions of movement from such points, and of forward directions of movement would be 1:1:1, respectively. *In such a case there could be no learning at all so far as frequency effects go.* But since every trial in the maze must end with a forward run reaching the food box, as well as begin with a forward run, these respective probabilities would become $x + 1/2$, $x + 1/4$, and $x + 3/4$. In our totals, then, the expectations would be $40\ (x + 1/2)$, $40\ (x + 1/4)$, and $40\ (x + 3/4)$; or $40x + 20$, $40x + 10$, and $40x + 30$. We actually got 88, 71, and 96, respectively, a very close approximation. The coefficients, 40 in each case, represent 4 trials *times* 10 blind alleys to pass in each trial.

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[2] For simplicity we assume that returns occur only at times of emergence by the animals from *cul de sacs*, an assumption which does not do great violence to the actual behavior of rats.

If x_1, x_2, x_3, ... x_{10} represent, respectively, the number of times that an animal gets successfully past blind alley *1*, *2*, *3*, ... *10*, and if for simplification we posit a condition such that whenever at any point the animal begins a return movement on emergence from a blind alley, it must continue the return to the starting place whatever other blind alleys may be entered on the return run, then according to pure probability laws $x_1 > x_2 > x_3 > \ldots . x_{10}$. Just how much greater in each case? Evidently, according to the foregoing, $x_2 = 3/4$ of x_1, $x_3 = 3/4$ of x_2, $x_4 = 3/4$ of x_3, ... $x_{10} = 3/4$ of x_9. But x_{10} equals the total number of trials[3] that the animal has made up to the point of consideration in the experiment, or the total number of times that it has reached the food box, since each trial has only one run past *cul de sac* 10. Hence, if

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[3] Trial is here used in the sense of a continuous effort ending only when the food box is entered.

$$\begin{aligned}
x_{10} &= n, \\
x_9 &= 4/3 \text{ of } n = 1.33n, \\
x_8 &= (4/3)^2 n = 1.78n, \\
x_7 &= (4/3)^3 n = 2.37n, \\
x_6 &= (4/3)^4 n = 3.16n, \\
x_5 &= (4/3)^5 n = 4.21n, \\
x_4 &= (4/3)^6 n = 5.62n, \\
x_3 &= (4/3)^7 n = 7.45n, \\
x_2 &= (4/3)^8 n = 9.97n, \text{ and} \\
x_1 &= (4/3)^9 n = 13.32n.
\end{aligned}$$

In general, in a maze with y blind alleys the number of times that the first would be passed in forward runs in n trials is $(4/3)^{y-1}$ *times* the number that the last would be passed, *i.e.*, $(4/3)^{y-1}n$.

Now, on the assumption above, it is evident that the number of entrances to the respective blind alleys will be to the number of times that they are passed in the forward direction as $(x_1 - 1/4) : x_1$, $(x_2 = 1/4) : x_2$. . . . . $(x_{10} - 1/4) : x_{10}$.[4] Substituting the values determined above for x_1, x_2, x_3, etc., we get the following ratios of blind alley entrances to forward runs past blind alleys in order from the first to the tenth:

$$\begin{aligned}
13.07n &: 13.32n, \\
9.72n &: 9.97n, \\
7.20n &: 7.45n, \\
5.37n &: 5.62n, \\
3.96n &: 4.21n, \\
2.91n &: 3.16n, \\
2.22n &: 2.37n, \\
1.53n &: 1.78n, \\
1.06n &: 1.33n, \\
n - 1/4 &: n.
\end{aligned}$$

Now when n equals any small number, as 1, 2, or 3, it is evident that the number of times of passing successfully a blind alley over that of entering it (*i.e.*, the practice-effect according to the law of frequency) is proportionately greatest for the *cul de sac* nearest the food box, and that it steadily decreases in order back to the first *cul de sac*. This would mean, on the basis of pure frequency factors in learning, that in general the nearest blind alley to the food box would be eliminated first, the second next, and so on. Elimination of all entrances to the last *cul de sac*—that nearest the food box—would then convert the maze in question for the given rat into a nine-blind-alley maze, elimination of the ninth *cul de sac* would make practically an eight-blind-alley maze, and so on, till the maze habit became perfectly established.

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[4] Each is passed 3/4 of the number of times it is encountered, and is entered 1/2 of that number. Since each trial has one extra forward run it is evident that the course past the blind alley has an advantage of 3/4 — 1/2, or 1/4, run or practice over the course leading into the blind alley. This advantage is not relative, but absolute; for an equal number of forward and back runs past any *cul de sac* gives equal frequency, as we have seen, for the two directions.

This would explain perfectly, then, a backward elimination of *cul de sacs* without any suppositions of "retroactive association," or of stamping-in effects of pleasure from eating the food, the effects varying inversely with the nearness of the pleasure. Since, however, the rat is not obliged to continue each return run to the starting place, and often does not do this, the mathematics of the above calculation is indefinitely complicated. We could go ahead and determine the probability of such complete returns from the second, from the third, from the fourth, etc., blind alleys; but such calculations would add nothing of further advantage to the theory we are testing. It is very certain, moreover, that the animal very early in the learning process eliminates most of the return movements.[5] In general, the following statement will suffice, and it finds support not only in theoretical determinations but also in results obtained by flipping coins as shown in the four illustrative trials tabulated in Table I: The greatest number of entrances to blind alleys occur in the part of the maze first to be passed through. This is because every animal reaching the starting place on a return must reverse its direction, while the contrary is true at the other end of the maze. Rats entering the food box cannot return into the maze. If the maze is one having many blind alleys, however, the animals may make comparatively many entrances also to *cul de sacs* in about the middle of the maze, so far as mere probability is concerned, for the chances of complete returns from distant parts of the maze are small. Near the food end of the maze the entrances to *cul de sacs* are fewer in number because (1) the probability is small that the animals will get to this part of the trial without making returns, and (2) there are no returns from the extreme end of the maze due to the fact that the food box holds all rats that reach this end. *Every blind alley must be passed in the forward direction at least as many times as the one nearest the food box—usually most of them are passed many more times than it is,—while this last one is never passed in the return direction* and hence is never entered from that direction. The other several blind alleys are passed generally in an increasing number of times as their distance from the entrance place in the maze decreases. Exceptions to this statement will, of course, occur; for example, Table I shows only one entrance to *cul de sac* 8 and two to 10. The law is a statistical law, dealing with probabilities, and the results of sufficiently numerous cases should conform to it. The result of this general law is, then, that the act of running past the blind alleys becomes more practiced—is more frequently performed—than that of entering them, and, to an even greater degree, than that of returning; and that the proportion of this excess practice in following the true path is greatest nearest the food box.[6]

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[5] Peterson, Jos. The Effect of Length of Blind Alleys on Maze Learning: An Experiment on Twenty-four White Rats. *Behav. Mon.*, Ser. No. 15, 1917. 24 ff.

This explanation, then, suggested by Carr[7] and later by Watson,[8] but here for the first time worked out more fully and applied also to the regressive elimination of blind alleys, seems to explain admirably on the basis of frequency effects, taken in a general way, (1) why entrances to the blind alleys nearest to the food box should be eliminated first, and why, in general, all *cul de sacs* should be eliminated in the order of their distance from the food box; (2) why the number of entrances to the several blind alleys should increase in the same order.[9] The explanation would hold, of course, as would all the above reasoning, only on the condition that all other factors influencing the choices at the various bifurcations of the maze—such as the length of the *cul de sacs* and their general direction with relation to the true path—remained equal at the different points.

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[6] This agrees with actual results obtained as published in the monograph referred to in the previous note.

[7] Carr, H. A. *Psychol. Rev.*, 1914, **21**, 161 f.

[8] Watson, J. B. *Behavior*, 1914, Ch. 7.

[9] To be considered on subsequent pages.

Any differences in such matters, such as are found in all actual mazes, will not affect adversely the explanation as a general principle; they can only disturb the accuracy of our predictions based on it in any given case.

What, then, can be said of this theory, that pure probability-frequency factors explain the rat's learning in the maze? In the first place, there is an inconsistency in the explanations based on the theory, which on closer examination seems seriously to limit the validity of the theory; and, secondly, rats do not as a matter of fact learn the maze in agreement with the expectations of the theory.

Let us take up the first objection. Assume that a rat on the first trial enters *cul de sac* 1, emerges from it and continues forward in the right direction, that it passes 2 and enters 3. Let us suppose that on coming out of 3 it takes the return direction. Frequency, then, will favor its entering 1 again, if it continue past 2, which would be a matter of probability. On emergence from 1 again it should go forward and once more enter 3. Pure frequency (and also recency) effects would therefore lead us to expect the animal to continue running from 1 to 3, 3 to 1, etc., indefinitely. As a matter of fact other control factors develop to throw the animal out of this routine. These may be either changing external circumstances or they may be varying intra-organic factors. *These conditions, then, become the directive factors in the learning.* When the animal is thus thrown out of the trial conditioned by frequency, probability may again determine the course in the part of the maze beyond the third *cul de sac*, but here again frequency effects would serve only to fix another circular type of response. Frequency does not seem to operate toward the elimination of errors, but only to stereotype action.

It may be argued that the effect of frequency (and recency) is not strong enough thus to fix wrong acts in the beginning of the learning process. More scope might thus be left for the operation of mere probability laws to show themselves in the early trials of the animal. This, however, would be tantamount to saying that learning did not take place in the early trials. If frequency is the determiner of the learning, the rate of its operation does not alter the case. Such an assumption, moreover, is contrary to fact; learning effects are marked in the first and second trials. The only escape from this difficulty to the theory would seem to be an assumption that frequency factors are wholly *nil* up to a certain point, after a given number of trials and successful arrivals at the food box, and that they then begin suddenly, or gradually, to operate,—an incredible hypothesis. It is evident from a careful study of individual records that frequency effects show themselves from the beginning of the experience of the animal in the maze, and that other directive factors are operative in bringing about learning in even as simple a case as this.

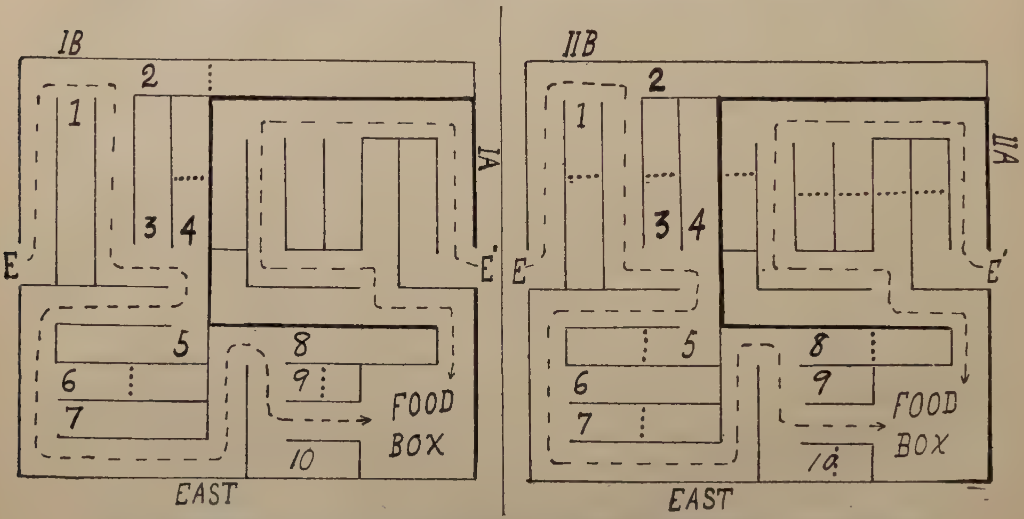

FIG. 2.—Mazes IB, IIB, and IA as used for present experiment. Dotted cross-lines mark the end of blind alleys in B-mazes. These mazes differ only in the relative lengths of blind alleys.

Our second objection is a question of fact. Do rats learn the maze in accordance with expectations based on frequency alone, or on frequency and recency? The question can be answered by a detailed examination of the actual records of several animals.

The method of tabulating individual records for detailed examination requires more space than can be expected for this article. A couple of samples of such tabulations up to points of nearly complete learning will be given, and results calculated from all the records at hand will be shown in more condensed form. The results are taken from experiments described elsewhere[10] on twenty-four white rats which were made to learn in different groupings two mazes of ten *cul de sacs* each and two of six each. For a description of the mazes, the procedure in the experiments, and of the animals the reader is referred to the other report. The results there given will be assumed to be familiar to the reader. In this connection we shall examine the records of seventeen of the rats in the mazes there described as IB and IIB (each with ten blind alleys), and IA (six blind alleys). Only the records of *un*trained animals, or animals without previous maze experience of any kind, will be considered. For convenience of reference the cuts of the mazes are here reproduced (Fig. II). Our present data are taken from animals running twice daily up to a point in the learning at which but few errors were made. The records of two animals in Maze IB and of one in Maze IIB were made useless for our present purpose by slight omissions in the record of the first day's trials.

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[10] Peterson, Jos. *Op. cit.*

Tables II and III show the several reactions of two rats tabulated in the manner explained in connection with Table I; the first is of an animal experiencing considerable difficulty (Rat 11), while the other is of one which much more quickly acquired the habit of keeping the correct path with but few errors (Rat 13). The records of the seventeen animals were all tabulated as those shown in the tables, except that the various "tallies" were first made with single lines. All records were then gone through carefully and the *critical choices* were marked in such ways as to indicate agreement or disagreement with expectations based on frequency and recency factors. Whenever an animal comes to a bifurcation in the maze that it has passed previously while going in the same direction, it is at what is called here a critical position, and its going into one of the rival alleys is a "critical choice." The second time that it arrives at *cul de sac* 1 on a forward run is an example. If it passed 1 the first time but now enters it, it goes *contrary* both to frequency and to recency expectations. The first return run in any section of the maze has critical positions only when the animal arrives at blind alleys which have been entered in the forward run. At such positions both frequency and recency factors favor entrance again, rather than a continuance of the return past this position in the true path. Entrance to such a *cul de sac* is *in accordance with* the expectations based on frequency and recency. There is no situation in which frequency factors operate alone with recency factors equally balanced, but there are situations in which the reverse is true. *E.g.*, suppose a given animal has entered *cul de sac* 2 (either in forward or in return runs, or both) twelve times, and also that it has passed 2 in the forward direction twelve times; the last of the two possible courses traversed is then the one favored by recency when 2 is approached by the animal going in the forwards direction. Frequency factors weigh equally for the two directions.

The following kinds of scores may be made by an animal at critical points: *Fr* = reactions favoring frequency but contrary to recency expectations; *Rf* = favoring recency, against frequency; *R* = favoring recency; *r* = against recency; *B* = favoring *both* recency and frequency; and *b* = contrary to both these factors. These symbols are used in the tables (II and III) here given to illustrate the treatment of the choices in the first three trials of each of the seventeen animals whose results are found in a condensed form on later pages. Choices scored "1" are uncritical choices.

In these tables only the first three trials are tabulated. The first trials are the important ones for the matter under consideration, in as much as the greatest changes in the behavior occur in the early part of the learning. The reason for this fact is obvious. In the early random stages of the learning any one of several single blunders is likely to throw the animal into confusion and bring about returns which lead to numerous other errors. It has been shown that the tendency to return is eliminated comparatively early in the process of learning the maze.[11] This fact is evidently responsible to a considerable extent for the very marked decrease in errors and time noticeable in the early trials. In the individual tables of the seventeen rats completed to the point of no errors in each record, it is found, as of course would be expected, that frequency-recency choices gradually increase in percentage, reaching at an early stage nearly 100%. Complete learning always gives 100% of such choices. *The meaning of this final preponderance of frequency-recency reactions is not that frequency and recency factors have brought about the learning*, but, more probably, *that some other factors have finally brought about the frequency-recency responses!*

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[11] See note 5.

TABLE II

RAT 11 MAZE IB

	MAZE PARTS																				
Direction	A	1	B	2	C	3	D	4	E	5	F	6	G	7	H	8	I	9	J	10	Food Box
Trial 1—Fd......			1	1	1	1	1	1	1	1	1		1		1	1					
Rt......				B	b	B	b	B	b	B	1		1		1						
Fd......					B	B	r		b	B											
Rt......	b	1	b		b	B	Rf		R												
Fd......		R	r	r																	
Rt......		B	b																		
Fd......			B		b		b		R	B											
Rt......								r	B												
Fd......									B	B											
Rt......		B	b	Fr	b		b	B	B												
Fd......			B	B	r		Rf		r	B											
Rt......			b	B	b	Rf	Rf		B												
Fd......				B																	
Rt......	b		R																		
Fd......			B	B	(Tak	en ou	t of m	aze af	ter 40	min.	Sat	still i	n 2 a	long	time.)						
Trial 2—Fd......			B	B	b		b	b	Fr	B											
Rt......						Fr	b		B												
Fd......							B	b													
Rt......	Rf		r	BB	b		Rf														
Fd......		b	Fr	B																	
Rt......	b		B																		
Fd......			B	B	b	r	Fr		r	B	b	b	r		B	BB					
Rt......								r	b		r		B		B						
Fd......									B		Rf		B	b							
Rt......								B	Rf		B		R								
Fd......									B	Fr	b	b									
Rt......						B	b		b		R										
Fd......							B		B	Fr	b		Fr		Fr	B					
Rt......								Fr	b		B		B		B						
Fd......									B	Fr	b		B		B	B					
Rt......											B		B		B						
Fd......											Rf	b	Rf		B		b	1	1	1	1
Trial 3—Fd......		b																			
Rt......	b																				
Fd......			Fr	Fr	Rf	r	B	b													
Rt......						B	b														
Fd......							B		B	Fr											
Rt......						B	Rf		Fr												
Fd......							B	Rf	B	B	b		B		B	b	Rf	B	B		R
Totals...........	5	6	9 7	14	7 5	11	11 9	11	13 11	13	8 6	3	7 5	1	6 4	6	2 0	2	2 0	1	2

1 = uncritical choice; R = in accordance with recency; r = contrary to recency; Rf = in accordance with recency and contrary to frequency; Fr = the reverse of Rf; B = in accordance with both frequency and recency; b = contrary to both frequency and recency.

TABLE III

RAT 13, MAZE IB

MAZE PARTS

Direction	A	1	B	2	C	3	D	4	E	5	F	6	G	7	H	8	I	9	J	10	Food Box
Trial 1—Fd.			1	1	1	1	1		1	1	1		1		1	1					
Rt.														1	1						
Fd.															B		b		1		1
Trial 2—Fd.		b	B	r	B		R		B	r											
Rt.						B	b	1	b												
Fd.							B		Fr	B	r		B		B		R	b	B	b	B
Trial 3—Fd.			B		R		B		B	Fr											
Rt.	b		b	B	b		R		b												
Fd.			B	R	Fr		B	b	Fr	B											
Rt.	R		b		b	Fr	r		R												
Fd.			B	r																	
Rt.	B		Rf																		
Fd.		b	Fr		b		Fr	b	Fr	B											
Rt.	Fr		Rf		Rf		r		B												
Fd.			B	r	B		B		B	B	b		B		B		B	b	B	Rf	B
Totals.	4	2	7 4	6	6 3	3	7 4	3	7 4	7	3 0	0	3 0	1	4 1	1	3 0	2	3 0	2	3

Tables II and III show many evidences of effects of frequency and recency factors. For instance, Rat 11 (Table II) returned rather regularly in the first trial from *cul de sac* 5; in the second trial it went into 8 and returned from there three times—once entering 8 twice in immediate succession—and got its forward orientation again rather regularly at 4; in the third trial blind alley 3 became effective in turning the animal forward from returns. It will be noticed that in this trial the animal entered 4 on the forward run, due likely to the frequent entrances to 4 in the second trial, and that this led to a confusion and a return to 3.

It should not be overlooked, however, that some of these repetitive entrances to blind alleys may be due more to the position of these *cul de sacs* in the maze (*i.e.*, to the physical circumstances of the learning situation) than to frequency and recency. This seems particularly to be true of *cul de sac* 5 in the B-mazes and of 4 in Maze IA. The effect of such physical conditions is obviously to increase considerably in the early trials the apparent effects of frequency and recency factors as these are determined in the present paper. Making allowance for such matters, we find that the *influence for learning* of frequency and recency in the early trials is surprisingly small. In many cases, as has been pointed out, the influence of these factors is *against* learning, other factors having to throw the responses out of frequency channels. These other factors are in all probability *visceral*; *they are larger bodily reactions away from monotonous repetitions which are unprofitable to the entire organism.* Of late these factors seem to have been neglected in psychology under the dominance of the too mechanistic associationism. Physiologists in work like that of Professor Cannon on emotional responses are reminding us that the organism after all reacts in a unitary way according to its own organic needs. It would seem that while pleasantness and unpleasantness are likely not in themselves causal factors in behavior[12] these affective "states" are plainly indicative of visceral participation—probably inhibitions and facilitations which we have yet to discover—in the learning process.

A detailed study of the seventeen individual records is interesting from several standpoints. It shows not only the dangers of generalizations based on averages, on time and "error" curves without detailed analyses, etc., but also many marked individualities of the several animals. Since it is impossible to say how much mere probability has operated in these early reactions to critical positions in the maze, these reactions are less certainly significant of individual differences than are differences in the more general behavior—speed, cautious attitudes, etc.—so frequently commented upon by various writers.

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[12] Peterson, Jos. Completeness of Response as an Explanation Principle in Learning. *Psychol. Rev.*, 1916, **23**, 153-162.

Summarizing in tabular form the results of all the *critical* choices of the several animals of the three groups, and, finally, of all together, we get the following tables (Tables IV-XIV):

TABLE IV

SUMMARY OF CRITICAL CHOICES OF FIRST THREE TRIALS BY SIX RATS IN MAZE IB

	Trial number	r[13]	b	Rf	Fr	R	B	Totals
Rat 13............	1	0	1	0	0	0	1	2
	2	3	5	0	1	2	10	21
	3	4	12	3	8	5	21	53
Totals..........	....	7	18	3	9	7	32	76
Rat 18............	1	5	13	0	1	2	16	37
	2	3	4	2	0	1	6	16
	3	4	7	2	5	0	11	29
Totals..........	....	12	24	4	6	3	33	82
Rat 12............	1	3	5	0	0	1	2	11
	2	8	8	0	3	0	10	29
	3	0	2	0	1	2	8	13
Totals..........	....	11	15	0	4	3	20	53
Rat 10............	1	4	6	1	0	6	6	23
	2	2	13	3	8	5	16	47
	3	1	2	1	1	1	8	14
Totals..........	....	7	21	5	9	12	30	84

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[13] r = contrary to recency expectations; b = contrary to *both* recency and frequency expectations; Rf = in agreement with recency, and contrary to frequency expectations; Fr = the reverse of Rf; R = in agreement with recency expectations; B = in agreement with *both* frequency and recency.

TABLE IV—*Continued*

	Trial number	r	b	Rf	Fr	R	B	Totals
Rat 9	1	1	2	0	0	0	3	6
	2	0	0	2	1	1	7	11
	3	3	28	6	12	6	46	101
Totals		4	30	8	13	7	56	118
Rat 11	1	6	16	4	1	4	25	56
	2	6	21	6	10	2	36	81
	3	1	6	4	4	1	12	28
Totals		3	43	14	15	7	73	165
Grand totals		54	151	34	56	39	244	578

TABLE V

General Summary of the Six Rats in Maze IB

Trial No.	r	b	Rf	Fr	R	B	Totals
1	19	43	5	2	13	53	135
2	22	51	13	23	11	85	205
3	13	57	16	31	15	106	238
Totals	54	151	34	56	39	244	578

TABLE VI

Table V Expressed in Percentage

Trial No.	r	b	Rf	Fr	R	B	Totals
1	13.3	31.8	3.7	1.5	9.6	39.2	100
2	10.7	24.8	6.3	11.2	5.4	41.5	100
3	5.5	24.0	6.7	13.0	6.3	44.5	100
Totals	9.3	26.1	5.9	9.7	6.7	42.2	100
	r + b = 35.4			R + B = 48.9			

TABLE VII

SUMMARY OF CRITICAL CHOICES OF FIRST THREE TRIALS BY FOUR RATS IN MAZE IA

	Trial number	r	b	Rf	Fr	R	B	Totals
Rat 7	1	5	3	0	0	2	1	11
	2	2	2	0	0	2	3	9
	3	3	6	0	0	1	5	15
Totals		10	11	0	0	5	9	35
Rat 5	1	0	1	0	0	1	0	2
	2	5	21	6	8	3	33	76
	3	0	7	0	2	0	14	23
Totals		5	29	6	10	4	47	101
Rat 1	1	5	3	0	0	0	1	9
	2	2	5	0	3	1	13	24
	3	0	0	2	0	2	3	7
Totals		7	8	2	3	3	17	40
Rat 8	1	1	2	0	0	0	3	6
	2	3	9	2	1	4	7	26
	3	2	0	1	0	0	3	6
Totals		6	11	3	1	4	13	38
Grand totals		28	59	11	14	16	86	214

TABLE VIII

GENERAL SUMMARY OF FOUR RATS IN MAZE IA

Trial No.	r	b	Rf	Fr	R	B	Totals
1	11	9	0	0	3	5	28
2	12	37	8	12	10	56	135
3	5	13	3	2	3	25	51
Totals	28	59	11	14	16	86	214

TABLE IX

TABLE VIII EXPRESSED IN PERCENTAGE

Trial No.	r	b	Rf	Fr	R	B	Totals
1	39.3	32.1	0.0	0.0	10.7	17.9	100
2	8.9	27.4	5.9	8.9	7.3	41.5	100
3	9.8	25.5	5.9	3.9	5.9	49.0	100
Totals	13.1	27.6	5.1	6.5	7.5	40.2	100
	r + b = 40.7			R + B = 47.7			

TABLE X

SUMMARY OF CRITICAL CHOICES OF FIRST THREE TRIALS, SEVEN RATS IN MAZE IIB

	Trial number	r	b	Rf	Fr	R	B	Totals
Rat 15	1	7	17	3	5	2	11	45
	2	1	1	1	1	0	9	13
	3	1	4	1	1	0	8	15
Totals		9	22	5	7	2	28	73
Rat 24	1	2	12	1	2	3	10	30
	2	2	8	0	3	3	10	26
	3	0	3	1	0	1	8	13
Totals		4	23	2	5	7	28	69
Rat 20	1	6	5	0	0	1	4	16
	2	2	1	1	0	2	7	13
	3	3	6	0	0	0	11	20
Totals		11	12	1	0	3	22	49
Rat 21	1	1	7	0	0	2	12	22
	2	2	8	3	5	2	17	37
	3	1	1	1	2	1	8	14
Totals		4	16	1	7	5	37	73
Rat 22	1	3	9	0	1	1	5	19
	2	4	4	1	4	3	7	23
	3	2	3	1	0	2	7	15
Totals		9	16	2	5	6	19	57
Rat 23	1	0	0	0	0	0	0	0
	2	4	20	0	1	3	17	45
	3	1	2	1	0	1	8	13
Totals		5	22	1	1	4	25	58
Rat 17	1	1	4	0	0	1	2	8
	2	4	16	2	0	3	14	39
	3	0	3	1	0	1	9	14
Totals		5	23	3	0	5	25	61
Grand totals		47	134	18	25	32	184	440

TABLE XI

GENERAL SUMMARY OF SEVEN RATS IN MAZE IIB

Trial No.	r	b	Rf	Fr	R	B	Totals
1	20	54	4	8	10	44	140
2	19	58	8	14	16	81	196
3	8	22	6	3	6	57	104
Totals	47	134	18	25	32	184	440

TABLE XII

TABLE XI EXPRESSED IN PERCENTAGE

Trial No.	r	b	Rf	Fr	R	B	Totals
1	14.3	38.6	2.9	5.7	7.1	31.4	100
2	9.7	29.6	4.1	7.2	8.2	41.3	100
3	7.7	21.2	5.8	2.9	5.8	56.7	100
Totals	10.7	30.4	4.1	5.7	7.3	41.8	100
	r + b = 41.1			R + B = 49.1			

TABLE XIII

GENERAL SUMMARY OF ALL SEVENTEEN RATS IN THE THREE MAZES

Trial No.	r	b	Rf	Fr	R	B	Totals
1	50	106	9	10	26	102	303
2	53	146	29	49	37	222	536
3	26	92	25	36	24	190	393
Totals	129	344	63	95	87	514	1232

TABLE XIV

GENERAL SUMMARY OF ALL SEVENTEEN RATS EXPRESSED IN PERCENTAGE

Trial No.	r	b	Rf	Fr	R	B	Totals
1	16.5	34.9	2.9	3.3	8.6	33.7	100
2	9.9	27.2	5.4	9.1	6.9	41.4	100
3	6.6	23.4	6.3	9.2	6.1	48.3	100
Totals	10.5	27.9	5.1	7.7	7.1	41.7	100
	r + b = 38.4			R + B = 48.8			

It will be noted that the summaries of the first three trials of the animals of each group approximate rather closely the results of all seventeen, so far as combined recency and frequency relations are concerned; *i.e.*, 38.4% *against* the expectations based on recency alone and on both recency and frequency, and 48.8% in *agreement with* the expectations on recency alone and on both recency and frequency. The differences of physical conditions in the three mazes used—slight in the case of the B-mazes, differences only in the relative lengths of the *cul de sacs* similarly located with respect to the correct path—do not show themselves much in these results. Of course, only a small number of animals were tried on each maze and the present results need corroboration by more extensive studies. It is obvious that there is a gradual increase with successive trials, in all three mazes, in the reactions agreeing with recency expectations or with recency and frequency expectations combined; and that there is a corresponding decrease in reactions violating such expectations. Table XV shows this tendency. It would seem from this table that the change is most rapid in the easiest maze, IA, as is to be expected. It cannot be too strongly pointed out, as has already been mentioned, that this increasing percentage of reactions agreeing with the expectations based on recency and frequency effects, as learning advances from the first random stages toward the establishment of a regular habit, cannot be safely regarded as evidence that learning is brought about by recency and frequency factors: our evidence seems to justify the contrary conclusion, that this increase in reactions

TABLE XV

SHOWING GRADUAL INCREASE WITH SUCCESSIVE TRIALS IN REACTIONS FAVORING RECENCY AND FREQUENCY EXPECTATIONS

Trial No.	Four Rats in Maze IA		Six Rats in Maze IB		Seven Rats in Maze IIB		All Seventeen Rats	
	r + b	R + B	r + b	R + B	r + b	R + B	r + b	R + B
1	71.4	28.6	45.1	48.8	52.9	38.5	51.4	42.3
2	36.3	48.8	35.5	46.9	39.3	49.5	37.1	48.3
3	35.3	54.9	29.5	50.8	28.9	62.5	30.0	54.4

favoring recency and frequency factors is the *result* of the learning. A completed habit must give 100% of such reactions.[14]

It is not contended here that our results show the effects of frequency and recency on behavior to be negligible. On the contrary, their effects are obvious in any detailed study of the rat's learning in the maze, pursued by the method of analysis here developed. But so far as the bringing about of the short cuts (the elimination of useless acts) in learning is concerned, recency and frequency factors do certainly not seem to play the important part that they have been considered to play in maze learning. It is but natural to suspect that the same thing will hold for other types of learning. It seems that we are in need of searching analyses of the detailed aspects of all sorts of learning. Our initial spurt of progress in the study of learning has passed and mere time, error, discrimination, and average attainment curves of general results can no longer solve the problems that we are coming to as soon as we begin more detailed studies.

So far as experimental evidence goes at present it would seem that maze learning by rats agrees in the main with the results to be expected on the basis of probability-frequency factors as their general results were pointed out in the early part of this paper; that is, that the blind alleys nearest the food box are first eliminated, and that entrances to blind alleys are greatest near the starting place in the maze and decrease for the successive *cul de sacs* directly with their nearness to the food box. Recent results published by Hubbert and Lashley[15] seem to agree with this conclusion, though these results raise other problems the solution of which is not yet made clear. Miss Hubbert found in an earlier research[16] no invariable sequence in the elimination of blind alleys, but the more recent article cited admits that "when averages of very large groups of animals are taken there does seem to be progressive elimination of errors for the food compartment to the entrance of the maze."[17] Miss Vincent's[18] and my own[19] results show in general the same progressive elimination of errors.

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[14] See an erroneous conclusion by Hamilton in his interesting monograph, A Study of Perseverance Reactions in Primates and Rodents. *Behav. Mon.*, Ser. No. 13, 1916, pp. 38-46.

[15] Hubbert, H. B., and Lashley, K. S. Retroactive Association and the Elimination of Errors in the Maze. *Jour. Animal Behav.*, 1917, **7**, 130-138.

[16] Elimination of Errors in the Maze. *Ibid.*, 1915, **5**, 66-72.

[17] These averages as given in the later article are, going in the order from entrance place toward the food box: 30.6, 26.4, 19.7, 19.7, 18.7, 8.3.

[18] Vincent, Stella B. The White Rat and the Maze Problem. IV. The Number and Distribution of Errors: A Comparative Study. *Jour Animal. Behav.*, 1915, **5**, 367-374.

Hubbert and Lashley classified the errors in the circular maze into those of wrongly passing a door (type I) and those of turning in the wrong direction (type II). The errors of type I they found to be eliminated in less than two-thirds the trials necessary for the elimination of those of type II. The serial backward elimination of errors of type I was found to agree in the main with results of the other studies cited in the preceding paragraph, but no such serial elimination of the type II errors took place. They find, in accord with our own results, that the animals seem to orient themselves to the maze as a whole, favoring in the several blind alleys the inward direction which in the circular maze is always toward the food box. If the individual reactions of each animal had been studied more in detail these experimenters would likely have found the explanation of the differences in the method of elimination of the two types of errors. Our results, in the monograph already referred to, show that the animal soon learns to keep its general forward orientation in the maze, and also that the final stages of the elimination of blind alleys are frequently accompanied by a confusion to the animal which results in entrances to *cul de sacs* nearer the food box, already eliminated. A study of the situation in the circular maze seems to suggest that the early development of the forward orientation tendency would tend to throw the animal into the blind alleys entrance to which constitutes errors of the second type. In every case a rat keeping its general forward direction and avoiding the error of type I would be thrown into an error of type II. This condition certainly would seem to invalidate the authors' general conclusion as to the relative frequencies of elimination of the two types of error. Moreover, since the rate of elimination is studied in terms of the number of trials required to avoid successfully the entrance to a blind alley, it must be recalled that the final trials for elimination of the *cul de sacs* first encountered will bring about confusions resulting in entrances to some of those already eliminated, further along the trail. From these confusions errors of type II would most probably result, for the reason already indicated. The matter seems to need further investigation. These difficulties make plain how necessary it is to avoid the fallacy of assuming—and these authors, I believe, do not assume this—that each response can be considered on its own account, rather than in relation to other reactions concerning vitally the welfare of the entire organism. It would seem that with a different arrangement of the relations of the two types of blind alleys in the circular maze, so that the objection here urged would be met, results in this maze would in general agree with those obtained in the use of other mazes,[20] showing that on the whole there is a progressive backward elimination of errors in the maze. There are, of course, many circumstances, making entrances to certain *cul de sacs* more probable than to others, that tend against this general rule. No maze in existence has *cul de sacs* all presenting equal difficulty to the animal.

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[19] Cited in note 5.

The writer believes that in spite of the shortcomings of the frequency factors as an explanation principle of maze learning, the general considerations which he has discussed in the first (the theoretical) part of this paper satisfactorily account for the progressive backward elimination of errors in the maze, to the extent that it actually occurs, and also for the fact that the number of entrances to blind alleys increases roughly with their distance from the food box. There seems to be no " retroactive association " necessary, as Hubbert and Lashley rightly conclude.

If frequency and recency factors play the unimportant part in actual *learning* that our present data seem to indicate, to what neural and physical conditions, then, must we look for the main factors that bring about the elimination of random acts and the *changes in behavior* characteristic of learning? The writer has attempted elsewhere to indicate in a general and tentative way the answer to this question. In support of his contention that our neural explanations have usually been so simple as to throw us into a mechanical associationism which finds difficulty in explaining the changes in behavior characteristic of learning; that neural processes are inconceivably complex so that the general consistency of the circumstances, organic and extra-organic, forces short-circuiting of impulses in the central nervous system,—in support of this position the writer is pleased to quote a few lines from Professor C. J. Herrick[21] which have come to his attention since the former articles were written:

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[20] Cf. Carr, H. A. Distribution and Elimination of Errors. (An abstract.) *Psychol. Bull.*, 1917, **14**, p. 58.

[21] *Introduction to Neurology*, 1916, p. 306. See also page 296 and Ch. XXI.

"Between the sensory projection centers and the motor areas are interpolated the association centers, and these are so arranged that all correlation, integration, and assimilation of present sensory impulses with memory vestiges of past reactions are completed, and the nature of the response to be made is determined before the resultant nervous impulses are discharged into the motor centers. Only such of the motor areas will be excited to function as are necessary for evoking the particular reaction which is the appropriate (that is, adaptive) response to the total situation in which the body finds itself. This arrangement of association centers in relation to a series of distinct motor areas provides the flexibility necessary for complex delayed reactions whose character is not predetermined by the nature of the congenital pattern of the nervous connections."

Through our inheritance from association psychology we seem to have fallen into a narrow, mechanical view which in the case of our own conduct belies our introspective reports, a view which is narrow and untrue not because it attempts to be biological as opposed to spiritualistic but because it so much neglects the larger visceral reactions with which we are just now becoming better acquainted. The reaction away from monotonous and unprofitable repetitions, of which we have found so plentiful illustrations in the rat's maze-learning, is similar to what we find in our own conduct. Professor Dodge, in his presidential address before the American Psychological Association, emphasizes a view in his treatment of the subject of fatigue which seems to agree with our own. On the particular point in question, the influence of general visceral demands, he says: "In my own case I have been interested in observing how every prolonged period of monotonous work like correcting papers, for example, finds before its close some insistent demand for interruption. If I successfully suppress one demand, more insistent ones arise, until finally effective voluntary reinforcement of the main task suddenly ends."[22]

SUMMARY AND CONCLUSION

Working on Professor Watson's suggestion, that probability determines the early reactions of the rat in the maze and that the principle of frequency finally determines which of the various random acts will survive, *i.e.*, that it brings about the learning, we have found by flipping coins that probability does afford an explanation of how the animal finally reaches the food box in the maze, but that it fails to explain alone or in connection with recency how the useless acts are eliminated. Recency and frequency factors do not seem to explain how the short-cuts in behavior characteristic of learning come about. Probability and the effects of recency and frequency factors supplemented by certain visceral directive factors, do, however, seem to account in a satisfactory manner both for the elimination of *cul de sacs* in a progressive backward order, roughly speaking, and also for the greater number of entrances to *cul de sacs* in the first part of the trail and for the general correlation between the number of such entrances and the distances of the respective *cul de sacs* from the food box.

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[22] Dodge Raymond. The Laws of Relative Fatigue. *Psychol. Rev.*, 1917, 24; 89-113. Quotation is from page 111.

Tabulations of the reactions of seventeen rats in their first three trials in three different mazes—six in one, four in another, and seven in the third—show that, contrary to certain current views, over 50% of the rat's early critical choices at bifurcations in the maze are the opposite of what would be expected on the basis of recency and frequency factors. Responses favoring expectations on recency and frequency increase and finally reach 100% when the learning is complete. This, however, is not evidence that these factors bring about the learning. The converse is true: the modification called learning increases frequency and recency responses. It is suggested that this may also be true of other types of learning.

There seems to be clear evidence of the operation in learning of visceral factors controlling, for the general demands of the organism, the associations which are formed. Choices at bifurcations in the maze are not predictable on the basis of frequency and recency alone as applied to individual responses; each response must be considered in the light of the whole situation to which the animal as a unitary organism is reacting. The elimination of random acts, of entrances to *cul de sacs*, seem to be comprehensible only on this basis. This seems to indicate that the laws of association are not the dominantly controlling factors that they have credit for being in current psychology.

An analytic method of studying learning in the maze is developed, one which may be applied to other simple types of learning when the necessary controls are available.

THE ALTERNATION PROBLEM

A Preliminary Study

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INTRODUCTION

In the discrimination experiment animals are required to choose between several paths according to some given temporal scheme. It is recognized that the animals may ignore the stimuli to be discriminated and solve the problem by reacting to this temporal order of presentation. This possibility is usually eliminated by several means:—1. By instituting a sequence of such complexity that the animals are unable to master it. 2. By varying the given temporal order after the problem is mastered; and 3, by removing the stimuli and requiring the animals to rely upon sequence alone. The control tests have almost invariably shown that the sequence factor is relatively insignificant in the solution of these problems.

The ability of animals to master given sequences of position habits has not been adequately investigated. Such a problem presents several aspects of interest:—1. The determination of the limits of complexity which a given animal can master. 2. The relative difficulty of sequences differing in kind and degree of complexity. 3. The possibility of discovering new aspects of the learning process. 4. The determination of the various conditions conducive to the development of such habits; and 5, the character of the sensori-motor mechanisms involved in such series of alternating habits.

This paper reports the results of an experiment which was designed as a preliminary attack upon the above program. Before designing and constructing an apparatus especially adapted for this purpose, it was deemed advisable to test a group of animals upon a simple sequence. For this purpose we utilized a piece of apparatus which had been employed in the study of a particular phase of the discrimination problem. The essential features of this discrimination box are represented in fig. 1. The center consists of a 2′ x 3′ rectangular area. Opening from this enclosure are two exits, R and L, each 4″ x 4″ in dimensions. These exits are separated from each other by a distance of 6″, and they open into two runways, A and B, both of which lead to the food box F. These paths to the food box can be closed by means of two sliding doors situated at C and D.

A group of eight white rats was tested upon a simple alternation between two positions habits. On each trial the animal was taken from the food box and placed by hand at the position marked by an arrow in the figure. Both position and body orientation were kept constant from trial to trial, the head of the animal being placed at the position of the arrow head equidistant from the two exits. On the first trial of each day the path leading from the exit R was left open, while the path from L was blocked. On the next trial L was opened and R blocked, and this procedure was repeated for each day so that the order of presentation may be represented by the schema of R-L-R-L-R-L, etc. The number of trials per day was varied from two to eighteen according to the condition of the animal and the stage of learning. Progress in mastery was measured in terms of the percentage of correct choices, and a choice was termed correct whenever the proper door was entered sufficiently to secure a body orientation along the length of the passage

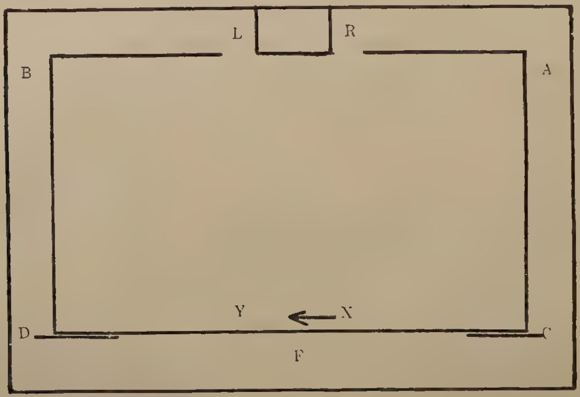

FIGURE 1.—Plan of apparatus. R and L, two exits; A and B, two pathways; C and D, sliding doors; F, food; Arrow, position in which rats are placed in apparatus; X and Y, two positions at which rats were placed in control tests.

way. The time devoted to a single run varied somewhat with the animal and the stage of mastery, but it became practically a constant after the first fifty trials. This time was determined for each animal for different stages of mastery. The average time per rat ranged from 21.5 to 25.5 seconds with a group average of 23. Of this time, 6.5 seconds were devoted to the run and 16.5 seconds to feeding and handling between runs.

ANALYSIS OF THE LEARNING PROCESS

All members of the group were able to master this simple alternation with a high degree of accuracy. A consistent record of 85% of correct choices for the group was obtained at the end of 600 trials. The number of trials per rat necessary to secure such a degree of proficiency ranged from 168 to 588, with a group average of 412. The number of trials for five of the eight animals closely approximated 450.

Three graphs representing progress in mastery are given in fig 2. The group curve is represented by the solid line. In its general features it is similar to the usual learning curve. The distribution of choices between the two exits is at first a matter of chance as the initial record is 50% of correct choices. The initial trials are more effective than the later ones though the curve approximates a straight line more closely than does the typical learning curve. There is some indication of the existence of a plateau beginning at the 340th trial. This phenomenon is to some extent a group artefact, though four of the eight individual curves give some indication of a plateau in this region. The individual curves exhibit some pronounced differences. Four graphs exhibit a relatively rapid initial ascent followed by a period of slower progress. Only one of these, however, approximates the typical learning curve. The curves for three animals exhibit an approximately straight line ascent; progress is uniform for all stages of mastery. One curve is quite unusual in this respect as it descends rather rapidly for 200 trials, then rises abruptly, and this period of ascent is followed by the usual slow progress. This curve is represented by the broken line graph of fig. 2. The dotted line curve represents the case in which the initial trials are relatively the most effective. These two individual curves represent the two extremes between which are to be found all degrees of gradation.

The animals were required in the initial trial of each day to choose the right exit in order to secure food. Alternation was the rule for the remaining trials of that day's test. Mastery of these initial trials thus represents a different type of problem from that involved in the subsequent alternation. For this reason separate records were kept of these initial trials and the results were plotted and the curve compared with that representing the mastery of the problem as a whole. 1. Mastery of this initial choice proved to be extremely difficult for the majority of the animals. Five rats consistently made poorer records for the first trial than for the whole day for all stages of learning. Only one rat found the initial choice to be easy and reversed the above relation. 2. Seven of the eight animals made poorer records for the initial choice at the middle of the learning period than at the beginning. With one exception the curves for the initial choice exhibit a pronounced descent for the first stages of mastery. 3. With four animals progress in the mastery of the initial choice was correlated with the degree of success for the day, although these choices were the more difficult. In these cases the mastery of the problem as a whole was apparently dependent upon the ability of the animal to get the day's sequence started properly. With the remaining four animals, these two aspects of the problem were apparently not related. 4. All animals finally succeeded in mastering this

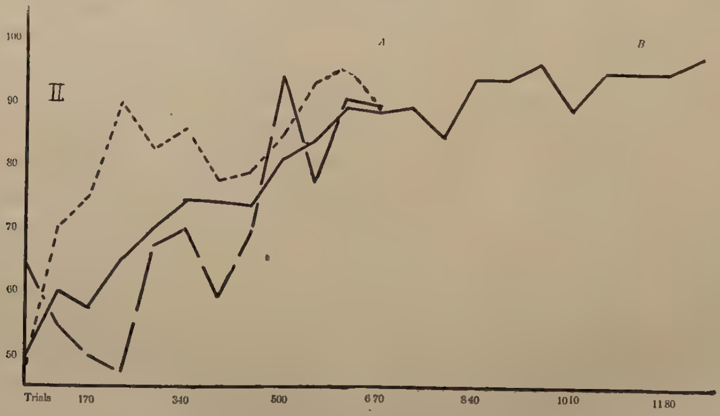

FIGURE 2.—Curves of learning. Solid line, group curve; broken lines, typical individual curves; curve from A to B, progress of group during period when control tests were given.

initial choice with a high degree of perfection. Some typical examples of these curves are given in figures 3 and 4. The solid line 1 represents the curve of learning for the problem as a whole, while the dotted curve 2 represents the course of mastery of the initial choice. Fig. 4 represents the exceptional case in which the solution of the two aspects of the problem were related and equally difficult. In fig. 3 the initial choice exhibited the greater difficulty; for some periods the two aspects were mastered together, at other times progress was antagonistic, while for most periods one problem was mastered independently of the other.

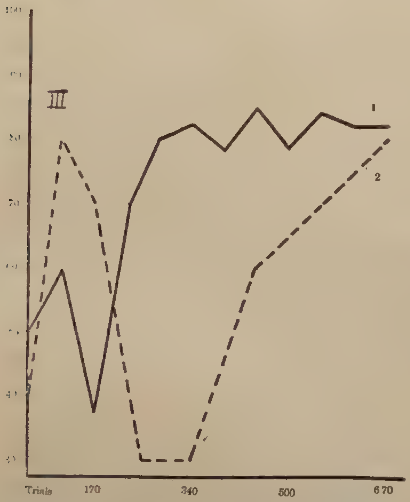

FIGURE 3.—Graph 1, individual learning curve; graph 2, curve of learning for mastery of initial choice.

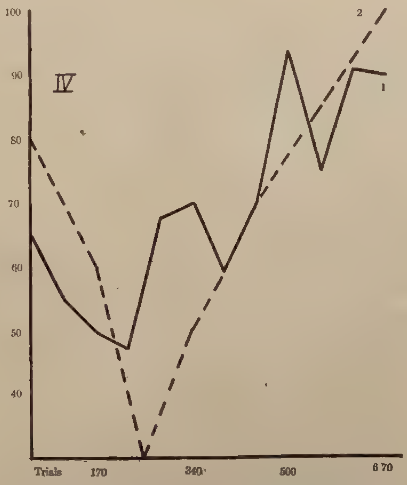

FIGURE 4.—Graph 1, individual learning curve; graph 2, curve of learning for mastery of initial choice.

Separate records were kept for the mastery of the two position habits. A comparison of the individual graphs reveals two general results. 1. Five animals found the mastery of the left position to be the easier. More correct choices of the left exit were consistently made for all stages of learning. The two positions were practically equally difficult for the other three animals. Mastery of the two habits was synchronous. 2. With four animals, the two habits antagonized each other's progress for the first half or two-thirds of the learning period. A rise in one curve was generally correlated with a fall in the other, and vice versa. The mastery of one path was made at the expense of an increased number of wrong choices of the opposite path. In the final periods of learning, however, the two habits were brought up to the same degree of perfection and progressed together. In all four of these cases the left path proved to be the easier and was mastered first. The reverse situation obtained for the other four animals. Progress in one habit was almost invariably associated with progress in the other. The two curves were thus similar in form. Typical examples of these relations are represented in figures 5 and 6.

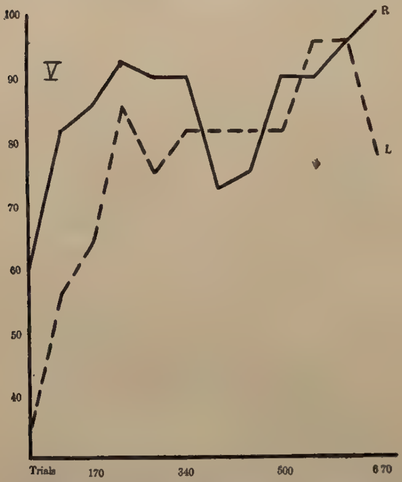

FIGURE 5.—Graphs R and L, curves of mastery of the right and left exits respectively.

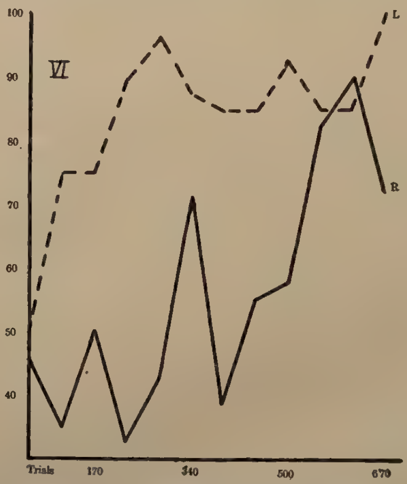

FIGURE 6.—Graphs R and L curves, of mastery of the right and left exits respectively.

The graphs L and R represent the progressive mastery of the left and right paths respectively. In fig. 6 the two habits antagonize each other's progress in the main, and the left position is the first to be mastered with any degree of perfection. In fig. 5 the two positions are mastered simultaneously, although the right habit maintained somewhat the higher degree of perfection for most stages of development.

During the solution of the problem, the animal may develop several modes of attack. 1. The rats may acquire a position preference, or they may distribute their choices equally between the two exits. A fixed preference for either of the two exits will give a percentage of 50 of correct choices and no improvement will be possible until the habit is broken. An equal distribution of choices will give a score of 50% with no improvement so long as the choices are a matter of chance. When the alternation system is mastered, the choices will still be equally distributed and a score of 100% will be attained. 2. The rats may develop the tendency either to repeat or alternate from the previous choice. An invariable repetition of the previous choice irrespective of whether it was correct or incorrect is equivalent to a position habit and it will give a score of 50% with no improvement. Alternation from the previous choice will give a score of zero if each day's initial choice was incorrect, while a perfect score of 100% will be attained if each day's sequence gets started properly. 3. The rats may also develop the tendency either to repeat or to alternate from the previous exit that gave food. The repeating tendency will necessitate a wrong alternation with a score of zero. The alternating tendency will solve the problem and give a score of 100%.

All possibilities thus reduce to two, the development of a position preference, or the acquisition of a habit of alternation and this alternating sequence of choices may or may not conform to the objective sequence. Our results were now analyzed and tabulated with the purpose of studying the development of these two tendencies.

The relative number of R and L choices, irrespective of their correctness, was determined for the successive stages of learning. The group exhibited a slight preference for the R exit for the first 100 trials. A pronounced L preference was now developed and this persisted with some degree of strength until the 500th trial, after which point the choices were equally distributed between the two exits. The L exit was consistently chosen in two-thirds of the trials for a period of 200 trials. The development of the L preference was confined to five of the eight animals, while the other three rats maintained a practically neutral attitude towards the two exits throughout the entire period of learning. The L preference began to develop somewhere in the period from the 50th to the 170th trial and it persisted for a period of 300 to 600 trials. Four of the five animals at times chose the L exit in 80% of the trials. The development of this preference may be both advantageous and detrimental to the mastery of the problem. It must certainly be detrimental in part because this habit must be broken before the problem can be mastered. The detrimental character of the habit is evident from the following facts. Each animal was ranked as to speed of learning. The three rats that developed no preference stood 1st, 2nd, and 6th in quickness of mastery. Among the five rats with a position preference those two which first eliminated this tendency were also the first to master the problem, while that animal which was the last to eliminate the tendency was also the last to complete the mastery of the problem.

The existence of these position preferences explains the relative speed of development of the two habits as previously described and illustrated in figures 5 and 6. The group of five animals that developed a preference for the left position contained the same individuals as the group that exhibited the greater progress in the mastery of the left path. The three animals that developed no position preference were the ones which mastered the two habits simultaneously. The distribution of the total choices between the two exits was practically identical with the distribution of the correct choices alone; this relation holds for the records of the group and each of the individuals. No matter how the total number of entrances are distributed between the R and L exits, the percentages of correctness for each are practically the same. In case a rat chooses the left exit 80 times in a series of 100 trials when it has developed an accuracy of 75%, the numbers of correct choices for the left and the right exits will be 60 and 15 respectively. The absence of a position preference will give 50 entrances for each of the exits in a series of 100 trials, and in this case the number of correct and successful responses will be equally distributed between the two paths. Since the percentage of successful responses is independent of the distribution of the choices, the number of correct choices of either exit must be a function of the frequency with which it is entered. In other words, the relative progression in the mastery of the two habits as illustrated in figures 5 and 6 is almost wholly a function of the position preferences which have been developed.

The rats may repeat or alternate from the previous choice and this alternation may or may not conform to the objective sequence. An analysis of the results reveals the following facts:—1. The repetitions and the alternations are practically equal in number for the first 50 trials. Evidently no animal came to the problem with a preference for either mode of choice. 2. Three rats maintained this neutral attitude for 150 trials, and then rapidly developed a pronounced preference for the alternating mode of attack. One animal immediately developed a slight preference for alternation and maintained this attitude for 400 trials, relapsed into a neutral attitude, and then rapidly developed the habit of alternation. Three animals rapidly developed a repeating preference for 300 to 400 trials, and then shifted quite rapidly to the opposite mode of attack. The remaining animal first developed a slight preference for alternation, shifted to the repeating tendency for 100 trials, and then perfected the habit of alternation in 300 trials. 3. The correctness of the choices due to repetition is a matter of chance. Each rat closely approximated a score of 50% of correct choices for every stage of learning. 4. The correctness of the choices due to alternation is at first a matter of chance. All rats approximated a score of 50% for the first 50 trials. Finally the rats learn to adapt their alternate choices to the objective series and approximate a score of 100% for this mode of attack. 5. Four rats rapidly learned the trick of adapting their alternate choices to the objective sequence. A score of 90% or better was attained in 150 to 250 trials. One of these individuals lost the trick for quite a long period and then remastered it. The other four animals at first increased their percentage of wrong alternations for 160 to 280 trials, and then quickly learned to adapt their choices to the objective series. 6. There is no correlation between initial ability to alternate and success in adapting this to the objective sequence. Of the four rats that immediately developed a preference for alternate choices, two succeeded in adapting these to the objective sequence and two did not. Of the four animals that decreased the initial number of alternate choices, two succeeded in adapting them to the given order of presentation and two did not.

Our problem thus presents four distinct difficulties which must be mastered:—1. The rat must learn to choose correctly the initial entrance for each day's trials. 2. The animal must learn to keep its choices equally distributed between the two exits, or, in other words, it must inhibit all tendency toward the development of a position preference. 3. The animal must learn to alternate its choices, and 4, it must further master the trick of adapting these to the temporal order of presentation.

The progressive mastery of the above aspects of the problem accounts for the peculiarities of the various curves of learning. An analysis of three typical learning curves into their four components will be given as illustrations.

The dotted line curve of fig. 2 exhibits the most pronounced initial rise and this rat was the first to master the problem with any degree of perfection. This animal also made the most rapid progress in mastering the initial choice, developed no serious position preference, belonged to the group which made the greatest progress in learning the habit of alternation, and was the first to learn the trick of adapting its alternate choices to the objective sequence.

Curve 1 of fig. 4 exhibits a rapid descent for 220 trials and this is followed by a normal rate of ascent until the problem was mastered. Likewise we find that the percentage of correct initial choices rapidly decreases for 250 trials and then increases at a normal rate. The animal also developed a position preference which reached its maximum strength at the 330th trial, and which was then quickly eliminated. The rat also developed a repeating preference up to the 390th trial, and then shifted very quickly over to the system of alternate choices. The percentage of correctness of the alternate choices decreased for 220 trials, and the animal then began to learn to adapt these to the objective sequence.

Curve 1 of fig 3 exhibits four aspects, an initial rise at the 100th trial, a pronounced fall at the 150th trial, a rapid rise to the 330th trial, and a subsequent plateau period. The corresponding percentage record of the initial choices is represented by curve 2 of the same figure. The animal first succeeded in choosing correctly, then failed dismally, and again succeeded. This rat also exhibited for 150 trials a position preference which was then quickly eliminated. The rat made no progress in increasing the number of alternations for 150 trials, and then practically perfected the habit in 150 trials. The curve representing the percentage of successful alternations is practically a replica of the learning curve of fig. 3.

The most important aspect of the problem is the ability to adapt the alternation to the objective sequence. The curves representing the percentages of successful alternations approximate most closely to the learning curves. Next in order of importance is the ability to alternate. The success of the initial choice is the least important factor; this fact is readily comprehensible from two considerations. The number of initial choices constitutes a very small proportion of the total, and the ability to alternate successfully depends but little upon the success of the initial choice except after the problem is practically mastered.

NATURE OF THE CO-ORDINATION

Each of the two alternating habits consists of an association between a movement and a certain stimulus. The two stimuli must fulfill at least one requirement; they must be presented in a given temporal order. Four possibilities exist:—1. The animals may be reacting in a differential manner to the two acts of adjusting the sliding doors, or to two different sensory conditions resulting from the adjustment. 2. They may be reacting to two different ways in which they are handled and placed in the starting position. 3. Each movement may be aroused by the cutaneous and kinaesthetic stimuli resulting from the previous act. This hypothesis assumes that the two acts are functionally related to each other in much the same way as are the two leg movements in locomotion. 4. The rats may be reacting to two different motor attitudes maintained during the act of feeding. The arrangement of the apparatus was such that the animals were forced to alternate between two opposite directions of approach to the food. It is possible that the body orientation involved in approach may be continued during the act of feeding, and hence that each run is preceded by a distinctive motor attitude toward the food.

The first possibility was eliminated by instituting tests in which both sliding doors were left open; in other words the rats were forced to react when the usual acts of adjustment were omitted. Again the doors were adjusted only after the choice of exits was made. Such control conditions did not decrease the percentage of correct responses.

The second possibility was tested in several ways. 1. The rats were placed in the box as usual with the exception that the head was placed at X when a choice of the left exit was demanded and at Y when the right exit constituted the correct response. The animals were thus compelled to start from two distinctive positions of such a character that a correct response necessitated a diagonal course from each position to the appropriate exit. The percentage of correct choices for the group under these conditions is represented at A in the graph of fig. 7. 2. The rats were now placed at the two positions, X and Y, in such a manner that a correct choice necessitated a direct course to the proper exit. The percentage result for the group is represented by B in the curve. 3. The animals were handled and placed in the usual position by Dr. Vincent. These results are represented in the curve at the points C. 4. The animals were subjected to normal conditions when the left opening constituted the correct choice, but whenever the right exit was to be chosen the animals were given a body orientation with the head pointing toward the right instead of to the left as under normal conditions. This orientation of the animal compelled the experimenter to place the rats in position with the left hand. The two choices are thus preceded by two distinctive methods of handling and two different orientations of the body. The results from this test are represented at the points D. 5. The rats were invariably given a head orientation toward the right instead of to the left as with normal conditions. This procedure involved a new method of handling and a new method of turning in starting for the exits. The results of the test are represented at the points E.

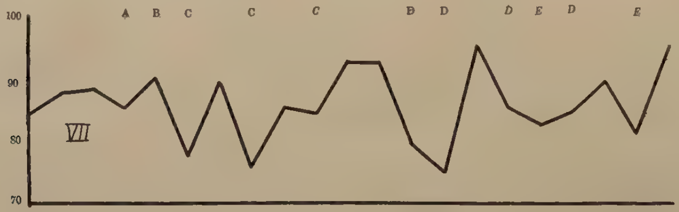

FIGURE 7.—Group curve representing the effect of the introduction of control tests.

Tests for normal conditions were interpolated among these control experiments. The records secured for these normal conditions are represented in the graph at those points not marked by letters. The value for each point of the curve represents the percentage of correct choices for the group out of 224 trials.

The following conclusions may be derived from the results of these control tests. 1. The introduction of the novel conditions decreased the number of correct choices for the group by 10%. 2. The alterations did not disturb two of the eight animals. The percentage of correct choices of the rat manifesting the greatest disturbance was lowered from 91 to 75%. No animal fell below a record of 75%. 3. The most disturbing conditions were those in which the animals were handled by strange hands and in which they were subjected to a new body orientation in starting. 4. The rats quickly adapt to these novel conditions. This fact is evident from an inspection of the graph. 5. The interpolation of these novel conditions interfered little, if any, with the progressive perfection of the two habits. At the beginning of the tests the animals had just attained a consistent group average of 85% of correct choices. At the end of the tests a record of 95% was secured. An improvement of 10% was thus attained during the period in which the tests were given. The perfection of the two habits during this period relative to the progress attained during the previous learning period is represented by the solid line graph of fig. 2. The curve up to the point A represents the progress attained during the learning period. The part of the curve between A and B represents the records secured from the tests for normal conditions which were interpolated among the various control experiments. The rate of progress during the control period is somewhat less than that obtaining for the period of learning. It is impossible to assert, however, that this decreased rate of learning is due to the introduction of the controls. 6. As previously noted the animals experienced difficulty in mastering the initial choice for each day's trials. This fact indicates that the animals were not relying exclusively upon sensory data derived from the mode of handling or the position in which they were placed in the apparatus. If such stimuli were efficacious, the first choice should have been no more difficult than the subsequent ones.

The above results prove rather conclusively that the animals did not rely exclusively upon the second class of stimuli. Neither does the slight decrease in efficiency resulting from the altered conditions prove that the rats are relying upon these stimuli in part, for any alteration of the subordinate and supplementary sensory environment may produce disturbances as readily as those aspects which are utilized as guides and controls. In other words, these altered conditions may have operated merely as sensory distractions. There are several considerations which indicate the truth of this hypothesis. The rapid adjustment to these changes is readily interpreted on this basis. The relatively poor records secured by the second experimenter were evidently due to fear. This emotional reaction was quite evident in the animal's behavior. The hypothesis is further supported by the fact that these changes did not materially effect the rate of progress in the final perfection of the habits.

The animals usually did assume and maintain a bodily orientation during feeding resulting from and characteristic of their direction of approach to the food box. However constancy of motor attitude was not the invariable rule. No attempt was made to control this factor nor were systematic records of bodily orientation taken. We are thus forced to the conclusion that the controlling and guiding stimulus to each choice consists either of the sensory aspects of the alternate act or of a motor attitude resulting from that act.

EFFECT OF INCREASING THE TIME INTERVAL

During the mastery of the problem, a period of 16.5 seconds was devoted to feeding and handling between runs. After the perfection of the association, this time interval between the two acts was gradually increased in order to determine whether the ability of the animals to make correct choices was dependent upon the length of this interval.

The results of this experiment are graphically represented by curve 1 of fig. 8. The percentages of correct choices are represented by the ordinate values while the various time intervals in seconds are distributed along the abscissa. The first four percentage values were secured for the normal time interval of 16.5 sec. All percentage values for the periods of 16.5 and 44 seconds inclusive are based upon a total of 224 trials. As the time interval is increased, the animals are given a greater opportunity for feeding, and necessarily fewer trials per day can be given. As a consequence the percentage values for the intervals of 50 to 95 seconds are based upon a total of 48 trials each. The following results are apparent from an inspection of the graph. 1. A gradual increase of the interval from 16.5 to 50 sec. exerts but little effect upon the accuracy of the act. The lowest record of correct choices for any animal for two successive days' trials was 82%. Six of the animals were able to make a record of 100% for a similar number of trials. 2. An increase of the interval up to 44 sec. did not disturb the accuracy of the act for normal conditions. A test for the normal time interval was interpolated after the group was given the 44 sec. interval. A group record of 96.5% was secured for a total of 288 trials.

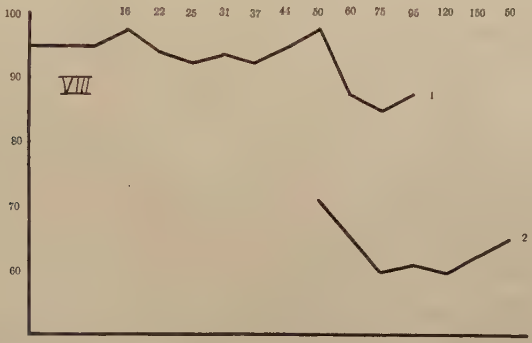

FIGURE 8.—Graph 1, percentage of correct choices for group with increasing time intervals. Graph 2, percentage of correct choices for group for large time intervals and the introduction of new conditions during the delay.

This value is not represented in the curve. 3. The number of correct choices suffers after a period of one minute is reached. This drop in the percentage values for the longer time intervals is not due to a diminished hunger motive as the number of trials per day was decreased from fourteen to six. The introduction of the longer intervals decreased the percentage values for the group about 10%. The lowest individual percentage record for the eighteen trials devoted to the three large intervals was 80, while the highest was 100. The decrease in the values was limited to five of the eight rats.

The experiment was continued with somewhat different conditions. After each trial the rats were allowed a few bites of food and then were placed upon an adjacent table. At the expiration of the given time interval, they were again placed in the apparatus for the succeeding trial. These conditions are radically different from those under which the problem was mastered. With the previous conditions the animals devoted themselves during the period of delay to the act of eating and they usually maintained a relatively constant position. On the table the rats were free to run around and react to whatever stimuli that may attract their attention. The purpose of the experiment was twofold. 1. We wished to determine the dependence of the choices upon the activities obtaining during the period of delay. To this end, we repeated the tests for the intervals of 50, 75 and 95 seconds. 2. We wished to continue the experiment with larger time intervals than the previous conditions permitted. With the new conditions the usual number of trials per day can be given even though very large time intervals are employed.

The results secured for these conditions are represented by curve 2 of fig. 8. The percentage value for the interval of 50 sec. is based upon a total of 1070 trials. The remaining values are each based upon a total of 100 trials. The following conclusions have been derived from these data. 1. The introduction of the novel conditions during the delay has decreased the percentage of correct choices by about 27%. The validity of this conclusion is readily apparent from a comparison of the two curves of fig. 8. 2. All of the animals were able to approximate a record of 70% of correct choices for the interval of 50 sec. 3. No improvement was manifested for the 50 sec. interval although the rats were tested daily for a period of 15 days. 4. The co-ordination was again disrupted for intervals greater than 50 seconds. The similarity of the two curves for the intervals of 50 to 95 seconds is striking. This fact indicates that the 60 sec. interval is a critical point. 5. Further increases beyond 75 sec. seem to be without effect. 6. The larger time intervals did not wholly destroy the functional efficiency of the co-ordinations for six of the eight animals. The group averages for these larger intervals are all at least 60%. Two rats made records of but 51 and 52% for the four large intervals. The percentage records of the remaining animals are at least 60%. The highest record was 70% and this score was made by two rats. Since these values are based upon a total of 52 trials for each rat, it is probable that some of these scores are significant. 7. The introduction of the long delays has tended to disrupt the act for the shorter intervals. The rats were finally tested again for the 50 sec. interval. Much poorer records were obtained than for the initial tests. The group record was decreased by 10%. Only four of the animals were now able to choose correctly for a score of 67% or better.

The experiment permits of the following general conclusions. 1. The guiding and controlling stimulus to each choice is constituted in part by the sensory aspects of the preceding act. A certain percentage of correct responses was obtained when all possibility of distinctive motor attitudes during the delay was wholly eliminated. Furthermore, any increase of the time interval beyond 60 sec. decreased the percentage of correct responses. 2. The rat may thus establish an associative nexus between a sensory stimulus and an act which are separated by a time interval of 16.5 sec., provided that relatively constant conditions exist during this period. 3. When an association has been established for a period of 16.5 sec., approximately one minute is the maximum time of separation of the stimulus and the response that may be obtained without disturbing their functional relation. 4. The functional efficiency of the coordination depends in large part upon the stability of the conditions that obtained for the period of delay. This fact supports the hypothesis that the guiding stimulus to each choice is constituted to a large extent by a distinctive motor attitude resulting from the previous act. The proof is not at all conclusive, however, for it is entirely possible to assume that the disruption of the act was due to the distractive influences of the novel sensori-motor conditions. 5. The efficacy of motor attitudes in the solution of the problem is indicated by the following facts. The relative disturbing effects of an increase of the time interval and the introduction of new conditions during the delay differ with animals. One may infer that some animals rely mainly upon the sensory aspects of the previous act as guides to conduct while other animals rely mainly upon motor attitudes. It is logical to suppose that those animals that place their chief reliance upon motor attitudes will learn the problem with the least effort because of the closer temporal contiguity of the stimulus and the response. As a matter of fact a positive correlation of .60 obtains between the ability to master the problem and the degree of disturbance due to the introduction of novel conditions during the interval of delay. In other words, those rats that rely mainly upon motor attitudes learn quickly and display the most disturbance when these motor attitudes are altered. On the other hand a negative correlation of .48 obtains between speed of learning and the degree of disturbance due to an increase of the time interval. Those rats that rely mainly upon the sensory aspects of the previous act in the solution of the problem are relatively slow learners and exhibit the greatest disturbance when this time interval between the stimulus and the response is increased.

FUNCTION OF VISION

The group of eight rats contained three blind animals. The records of the two groups were compared. The individual records are so variable and the numbers in each group are so few that it is impossible to make assertions with any degree of confidence. In general the group differences that exist are so small that they may well be due to chance or individual differences. Consequently the data as given justify the following negative conclusions. 1. The presence of vision did not influence the rate of learning. 2. No differences in the type of curve were apparent. 3. There were no manifest differences as to the interrelation of the R and the L habits. 4. No assertions can be made as to any differences of ability in mastering the initial choice for each day, or as to the relation between this choice and the day's success. 5. No differences were manifested in the mode of attack, or the ability to adapt the alternate choices to the objective sequence. 6. The groups did not differ as to the relative reliance which they placed upon the two sets of guiding stimuli. 7. No assertions can be made as to any differences of ability in solving the problem of increasing intervals of delay. It is of course possible that some of the above conclusions will need revision provided larger groups of animals are tested.

Two differences were detected. 1. The blind animals were somewhat the slower in movement and expended more time in making each run. The average time values per run were 6 and 7.2 seconds for the normal and the blind animals respectively. 2. In the later stages of mastery, the normal rats frequently turned immediately after entering the blocked path. The blind rats did not manifest this type of behavior. When wrong choices were made, the blind animals did not correct their mistake until actual contact with the closed door was effected. This differential behavior indicates that the normal animals frequently used visual data in reacting to a blocked pathway.

SUMMARY

All rats succeeded in learning to make alternate choices between two exits. The problem proved to be rather difficult for these animals.

The problem is a complex one consisting of four components which are stated in their order of importance. 1. The rat must learn to adapt its alternate choices to the given order of presentation. 2. The system of making alternate choices must be acquired. 3. The rat must resist the tendency of developing a position preference. 4. There is the final difficulty of choosing correctly in the initial trial of each day's test,—of getting the day's sequence started correctly.

These four aspects of the problem constitute to some extent independent difficulties in the early stages of mastery; progress in mastering one component does not necessarily depend upon the animal's ability to overcome the other difficulties. The four factors were mutually related in the case of some individuals, but there is no *necessary* dependence inasmuch as they were unrelated with some animals.

Animals differ greatly in their rate of progress in mastering each of these component elements of the problem. The curve of learning for the problem as a whole may be regarded as a combination of the four curves representing the mastery of the four components. The complexity of the problem, the independence of its parts, and the variability of the animals in mastering each part make possible a wide range of individual differences in rate and method of learning.

The final co-ordination consists of an association between each act and the sensory aspects of the preceding act as well as a distinctive motor attitude resulting from the same. The relative efficiency of the two stimuli in determining each choice varies with the individual. The problem was mastered quickest by those animals that relied mainly upon the factor of motor attitudes in making their choices. This fact suggests the hypothesis that the speed of learning is to some extent a function of the degree of temporal contiguity between the terms to be associated. Since the animals relied in part upon the sensory aspects of the preceding act, we are forced to conclude that a rat can establish an associative nexus between a stimulus and a response separated by a time interval of 16.5 seconds, provided that relatively constant sensori-motor conditions prevail during that interval.

The rate and mode of learning are apparently not dependent upon vision. Rats with vision exhibited the greater speed of movement and occasionally corrected their wrong choices in terms of visual stimuli from the closed doors.

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